

T-VS 4

components of productivity
of Mediterranean-climate regions
basic and applied aspects
edited by N.S. Margaris and H.A. Mooney

Components of productivity of Mediterranean-climate regions
Basic and applied aspects

Tasks for vegetation science 4

Series Editor

HELMUT LIETH

University of Osnabrück, F.R.G.

Components of productivity of Mediterranean-climate regions

Basic and applied aspects

*Proceedings of the International symposium on photosynthesis,
primary production and biomass utilization in Mediterranean-type
ecosystems, held in Kassandra, Greece, September 13-15, 1980*

Edited by

N. S. MARGARIS and H. A. MOONEY

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Preface by the T:VS Series editor

Tasks for Vegetation Science adds with this volume another category of vegetation treatments to the series. While the first volumes were contributed by individual authors or were translations from other languages, the present volume, No 4, deals with one specific vegetation type which is investigated by many competent researchers from different angles.

The value of such treatment is obvious. Besides the usual information about the ecology of one specific vegetation type the reader gets a variety of supportive information and suggestions for the application of his work.

Drs. Margaris and Mooney undertook the commendable task of organizing a symposium on Mediterranean Ecosystems near Thessaloniki in Greece. The content of each paper was discussed at that meeting. The discussions have been excluded from the book, but many suggestions were included in the papers by the individual contributors.

Although contributions from many areas of Mediterranean type vegetation of the world are included, the main focus is on vegetation of the Mediterranean area itself.

It will most likely be this type of symposium that will enhance our insight into the functioning of ecosystems. We suggest therefore that similar symposia be organized for other vegetation types.

The two organizers of the symposium, who are the editors of this volume, deserve much credit for this undertaking. We hope that more symposia of this type can be organized and prepared for publication in the T:VS series.

Osnabrück, June 1981

H. Lieth

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INTRODUCTION

Our knowledge of the functional characteristics of the plants of mediterranean-climate regions has increased greatly in the past decade. In recent times the possibility of large-scale utilization of biomass for energy from these regions has been proposed. In order to assess the feasibility of these proposals we must consider the productive structure of these plant communities and how they vary through time and space. This symposium was an attempt to examine our recently acquired basic knowledge of the environmental limitations on the productivity of Mediterranean plant communities in relation to the consequences of the possible utilization of these communities for energy and chemicals. Specifically in this book we examine the mechanisms by which plants of mediterranean-climate regions maintain their productive capacity under the prevailing conditions of summer drought and winter cold. We consider the characteristics of leaves, their history, morphology and plasticity. Evergreen sclerophyll leaves are common to the dominant plants of all mediterranean-climate regions and thus they have significance in terms of enhancing carbon gain and water-use efficiency as well as ensuring survival under the prevailing climatic conditions.

Communities of mediterranean-climate regions have a relatively low annual primary productivity as compared to temperate and tropical forested areas. The basis for this low production resides in both the environmental limitations on the photosynthetic process as well as the particular allocation patterns of the dominant plants, such as high allocation to roots which are characteristic of perennial plants of mediterranean-climate areas. The particular environmental limitations of photosynthesis are examined in this book in some detail as are carbon allocation patterns. In addition we view how pollutants, such as SO_2 , effect the productivity of these plants. A distinctive feature of mediterranean-climate regions is the high frequency of fires. These fires have a large effect on the nutrient balance of the habitat which in turn affects subsequent community productivity. The presence of stands of known dissimilar post-fire ages in most mediterranean-climate regions provides a good basis for estimating annual biomass accumulation as well as for viewing the dynamics of change of nutrients within these ecosystems.

Knowledge from all of above areas is necessary to provide a sound basis for evolving management schemes for possible utilization of biomass for energy and chemicals.

This book is result of a symposium held in Kassandra, Greece during September 13-15, 1980. One of the principal sponsors of the symposium was the UNESCO Man and Biosphere Program (MAB). The MAB program has one of its major goals the utilization of basic ecological information for the development of sound management policies for the earth's ecosystems. Hopefully the results of this symposium are a contribution toward this objective.

N.S. Margaris (Thessaloniki)

H.A. Mooney (Stanford)

PART ONE

LEAF MORPHOLOGY

Leaves are the principal sites of light interaction, gas exchange, and transpiration. They contain the complex structures involved in CO_2 fixation as well as other major metabolic processes. Leaves expose a relatively large surface area (2 to $3 \text{ m}^2 \text{ m}^{-2}$ in mediterranean-type ecosystems) to the fluctuations of the physical environment, and therefore it can be expected that analyses of leaf morphology will elucidate the interrelations between leaf structure and the specific characteristics of the mediterranean-climate environment. A summer drought of several months, leaf temperatures that may reach 50°C and drop in winter sometimes below freezing, and low levels of available nutrients are the main factors of the mediterranean-type environment that can be expected to have had an impact on the evolution of leaf structure.

Two main modes of adaptation have evolved in these regions. One is the soft and relatively thin leaves with high photosynthetic capacity per unit of leaf area which function as long as soil moisture is available. They dry at the end of the growing season. This drought-avoiding behavior is characteristic of the annual vegetation, the perennial cryptophytes and the summer-deciduous shrubs. This mode is in contrast to the sclerophylls of those shrubs and trees that have given the special physiognomy to the mediterranean-climate areas of the world. Surprisingly little information is available regarding the longevity of the foliage of the mediterranean-climate vegetation.

These two main types of foliage adaptation to water stress represent the extremes. We can expect that thorough morphological studies will reveal a broad range of structures closely related to the specific microclimatic conditions of the growing site. For example, structural differences between sun and shade leaves have long been known; however, little attention has been paid to the quantitative relation between light interception and cuticle development in the canopy of individual shrubs. Specific physiological parameters, like leaf resistance of CO_2 -fixation rates, are measured with relatively few samples and the results intergrated over whole shrubs or even research sites. More quantitative data on structural leaf characteristics could augment the basis for such extrapolations. There can be no doubt that plant structure is the result of evolution under the selective pressure of the intergrated environmental conditions. Understanding morphology and its dependence on the physical conditions of the growth site should provide the key for an understanding of ecosystem function. The papers that follow are a contribution toward such a goal.

F. Catarino (Department of Botany, University of Lisboa, Portugal) and

J. Kummerow (Department of Botany, San Diego State University, U.S.A.)

MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF THE MEDITERRANEAN EVERGREEN SCLEROPHYLL, CERATONIA SILIQUA, TO DIFFERENT LIGHT INTENSITIES

F. M. CATARINO, O. A. CORREIA, E. WEBB, M. DAVID (Department of Botany, University of Lisbon, Portugal)

1. INTRODUCTION

Mediterranean evergreen plants although basically xerophytes can exhibit several different strategies (Walter, Kreeb, 1970). Sclerophylly seems to play an important role in the "adaptation" of these plants to the natural climatic changes of mediterranean areas (Stocker, 1960). According to speculative classical work of earlier eco-physiologists, sclerophylly was envisaged as an adaptative mechanism for decreasing transpiration. However there is also evidence that sclerophylly structure vitally affects energy interception and dissipation. Moreover, sclerophylly characteristics of mediterranean plants usually show marked developmental plasticity (Thoday, 1953) leading to a canopy arrangement which ensures optimal photosynthetic capacities as long as water is available to plants. Ceratonía siliqua is a moderate sclerophyll species that seems well adapted to a wide spectrum of environmental conditions of the true mediterranean climate (Catarino, Bento-Pereira, 1976). The leaf anatomy of this species shows a compact palisade parenchyma, protected on both sides by thick-walled epidermis. A thick cuticle over each epidermis provides the leaves with an efficient defense against desiccation. According to the conditions of water availability and light intensity prevailing during morphogenesis and expansion of leaves, very profound changes in general leaf structure, cuticle development, stomatal density and degree of sclerophylly are observed. These changes certainly affect the photosynthetic capacity of plants, the carbon apportionment to shoot and roots and general biomass production. In the present study we analysed the effect of four levels of light intensity in controlling expression of several

physiological traits of young plants of Ceratonía. We hope to consider these management of traits in inducing resistance to damage during field transplantation. Among general physiological traits the following are assumed to be critical: (i) resistance to water transport through stomata and cuticle, (ii) development of an efficient root system, (iii) metabolic pattern of CO₂ fixation and leaf expansion and arrangement (Moreira, Matos, 1979). We have compared stomatal behaviour as affected by water potential and temperature. We have also studied the general growth patterns and carbon allocation in plants cultivated under each light level. Because of the economic importance of Ceratonía, we think that the data presented here may contribute to the optimization of nursery management of young plants prior to field transplantation when future programs of reforestation of arid lands in mediterranean climates are considered.

2. MATERIAL AND METHODS

Seeds of Ceratonía siliqua were sown directly in plastic pots, 15 cm diameter, filled with a mixture of equal parts of a loam soil and turf (pH 6.5) in December 1979.

The plants were kept during all the experiment under green-house conditions of Lisbon Botanical Garden (Fig. 1). The plants were watered with distilled water and at two week intervals, received 30 ml of Hoagland nutrient solution (Hewitt, 1966).

2.1. Light treatment. Pots with germinating seeds were divided into four groups. Group 1 received full light intensity. Group 2 (80% light) was located in a darker place in the green-house, close to a vertical stained glass wall that reduced light intensity. Group 3 and 4 (50% and 10% light) were placed under cubic frames covered with several

sheets of neutral green plastic mesh (1 mm) in order to obtain the desired level of radiation, (Fig. 1).

2.2. Stomatal parameters. Measurements of stomatal frequency were made in four leaflets of fully mature leaves of the 5th node. In each leaflet lower epidermis replicas were obtained at four locations using a commercial nail polish. Six random microscopic fields were counted from each replica. The stomatal resistance to water vapour diffusion was measured using a Lambda diffusion porometer Ll-60.

2.3. Hydromorphological indices and water potential. Measurements were made of 10 discs of mature leaves of the 5th node. For maximal turgidity the discs were kept for 4 hours over humid chambers formed by holes on a sponge plate saturated with distilled water. After fresh weight determination the plant material was dried for 48 hours in an oven at 90°C.

Water potential was determined in a Scholander pressure chamber according to Slavik (1974), using single leaflets adapted to slit openings in the rubber disc of the apparatus.

2.4. Growth analysis. After 7 and 9 months of cultivation 5 plants of each group were carefully removed from the pots and divided into leaves, stems and roots. Dry weights were determined by drying the material in an oven to constant weight. For leaf area determination the outline of the leaves of each plant was drawn on sheets of homogeneous paper and the corresponding areas were determined by weighing.

2.5. Anatomical observations. Free hand sections of leaflets of each treatment were obtained and stained with Sudan III. A fluorescence microscope was used on cuticle observations. A Scanning Electron Microscope (University of Aveiro, Portugal) was used for the upper and lower epidermal observations. The specimens were coated with a thin layer of carbon and gold-palladium.

2.6. Chlorophyll content. Chlorophyll determina-

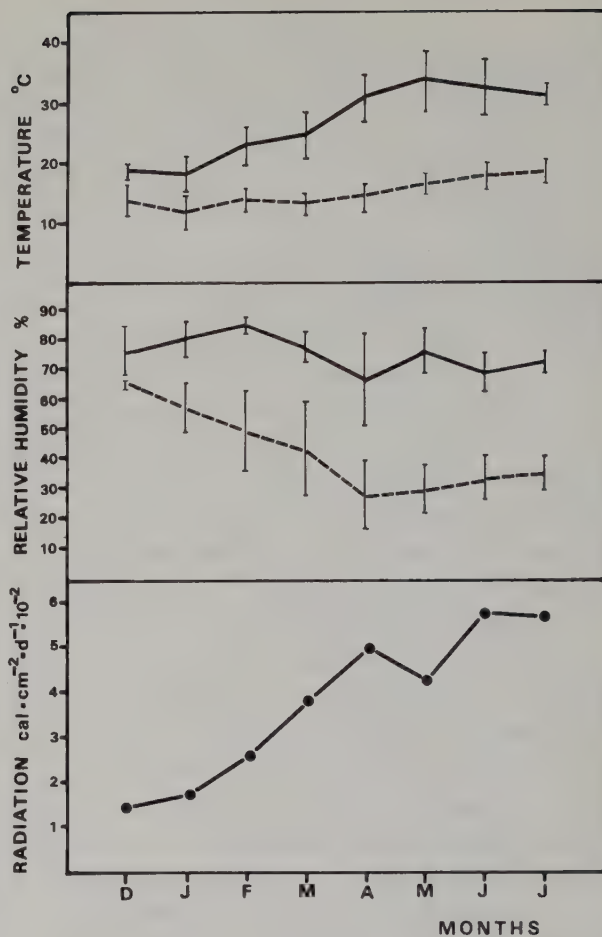


FIGURE 1. Mean monthly values of temperature (max. and min.), relative humidity (max. and min.) inside green-house. Values for global radiation are referred to outside conditions.

tions were made according to Ozerol and Titus, 1965, using leaf discs extracted in methanol. The absorbance readings were made at 651 nm and 664 nm.

3. RESULTS

3.1. Leaf morphogenesis as affected by light intensity.

3.1.1. Leaf anatomy. Under our experimental conditions germination occurred simultaneously in all treatments. Cotyledon leaves which are long-lived in *Cerantonia* did not exhibit differences in morphology with light intensity treatments. Differences in size, colour and thickness were apparent in the

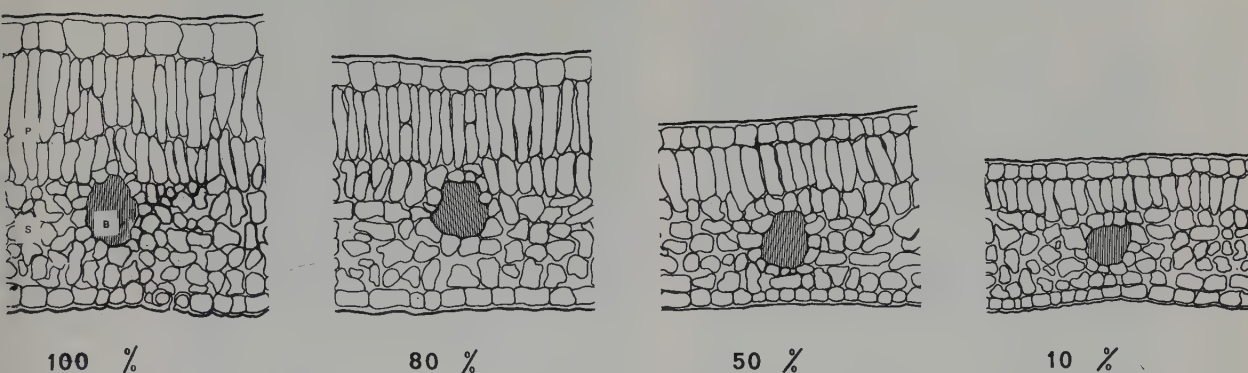


FIGURE 2. *Ceratonia siliqua*. Scheme of leaf cross section. P: palisade parenchyma. S: spongy parenchyma. B: bundle. Leaves grown under different irradiances as indicated.

true leaves as soon as each leaf fully expanded and matured. The observations reported here refer only two mature leaves of the 4 - 5th node number for all treatments. The gross leaf anatomy is shown in Fig. 2.

Clearly the thickness of leaves is well correlated with light intensity, full light producing the thickest leaves and 10% light regime the thinnest ones. Differences in leaf thickness occur not only in the lamina but also in the leaf rachis and in pulvinar structures at the base of each leaf and leaflet. Leaves of high light-grown plants with better developed pulvinar seem to react more efficiently in closing the leaf and changing leaflet angle when plants are subjected to drying. Changes in leaf thickness are mainly due to a difference in development of palisade parenchyma. Thicker leaves possess two to three layers of well packed palisade cells whereas thin leaves have usually one layer of palisade cells which are loosely packed. Epidermal cells are thick-walled and wall thickness is more pronounced in high light treatments.

3.1.2. Stomatal frequency. Fig. 3 shows the frequency of stomata per square millimeter. It is evident that light induces the highest densities approaching 200 stomata per mm^2 . Similar figures have been reported for mature *Ceratonia* plants growing in Lisbon area by Catarino and Bento-Pereira (1976).

Fig. 4 shows the outlines of lower epidermis cells of each treatment obtained by camera-lucida drawing of polish replicas.

3.1.3. Cuticle development and cuticular waxes. High light intensity induces thicker cuticle development. Thicker cuticle development seems to be directly related to thicker leaves.

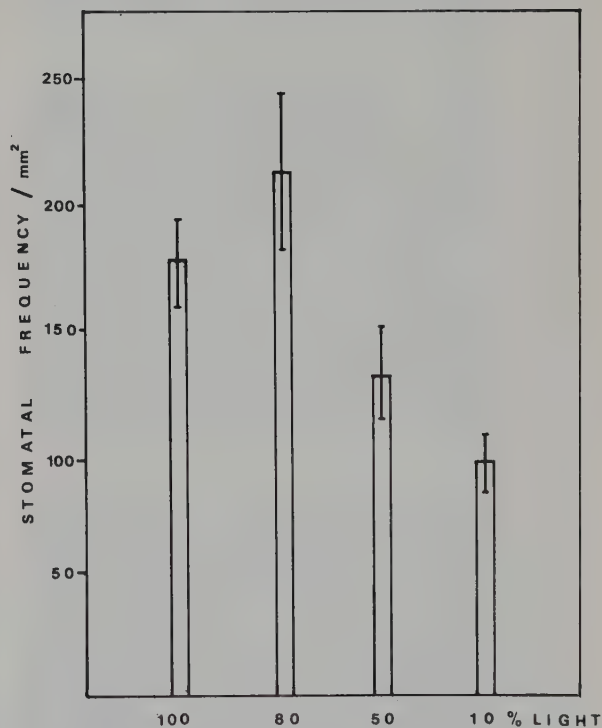


FIGURE 3. Stomatal frequency per square millimeter of *Ceratonia* leaves grown under different light intensities.

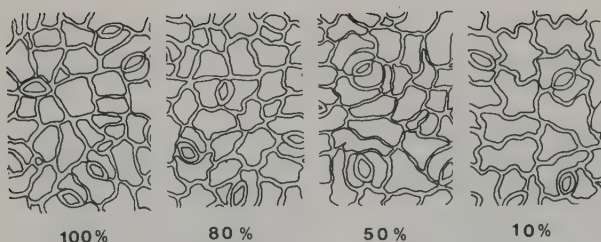


FIGURE 4. Cell outlines of lower epidermis.

Besides providing overall protection to the epidermis, plant cuticles seem to act as barriers to water and CO_2 diffusion. Recent evidence (Schonherr, 1980) indicates that regulation of water permeability depends on cuticle composition and structural arrangement rather than in cuticular thickness. With electron scanning microscopy it is apparent that both epidermal layers are covered with clumps of wax platelets (Fig. 5.a and 5.b).

At least in plants grown in high light intensity the cuticular surface is wavy, having scale like structures. Epicuticular waxes are denser in the lower epidermis. In our material, and dependent of our present methods for sample preparations for scanning microscopy, wax structures may occur as amorphous clumps of rods or more frequently, platelets arranged in arborescent crystalline like structures.

3.1.4. Chlorophyll content. Fig. 6 shows chlorophyll content of leaves of the four treatments. Chlorophyll content sharply decreases as the light intensity also decreases. When expressed on a fresh weight basis chlorophyll content follows an inverse trend, due to the thin leaves of low light plants, (Table I). The values are means of 6 replicates for each treatment when the plants were seven months older.

3.2. Water potential and resistance to water vapour diffusion.

3.2.1. Diurnal changes of stomatal resistance and water potential. Fig. 7 shows the daily course of stomatal diffusion resistance and

water potential in well watered individual plants. Measurements were performed under the same environmental conditions as those experienced during plant development. Leaf water potential varied from ca. -10 to -25 bar during the daylight hours. Predawn water potentials averaged -10 bar. The diffusion resistance of leaves is inverse by related to water potential. Predawn are very high but resistance rapidly decreases at sunrise to values less than 1 s.cm^{-1} in plants grown under strong light or to an average of 3 s.cm^{-1} in the low light plants. Some oscillation in the resistance may indicate a tendency for mid-day closure of stomata. However, this tendency was not found in the plants grown under high light. The oscillations which also occur in the water potential determinations may indicate inhomogeneity in the water status and stomatal behaviour among different leaves of the same plant.

3.2.2. Changes of stomatal resistance at different temperatures and water potential. The plants from each light treatment were subjected to moderate drought and transferred 24 hours before the measurements to a growth cabinet with day-light fluorescent tubes giving about 10 000 lux at the plants level. Groups of three plants from four levels of light were used in the stomatal resistance determination for each low (15°C), median (23°C) and high temperature (30°C) treatment. Values shown in Fig. 8 are means of replicate measurements done in three plants, between 10 and 15 hours. It can be concluded that the degree of stomatal resistance depends both on temperature and water status of the leaves. At low temperature higher resistance values were recorded for all plants.

At 30°C the stomatal resistance seems to increase specially in plants undergoing some drought stress. Surprisingly under low water potential 100% light grown plants exhibit at 23°C rather low resistance values compared with the values at both lower and higher temperatures.

3.2.3. Cuticular resistance. Due to methodological problems of ascertaining if stomata are tightly closed, measurements of cuticular resistance were

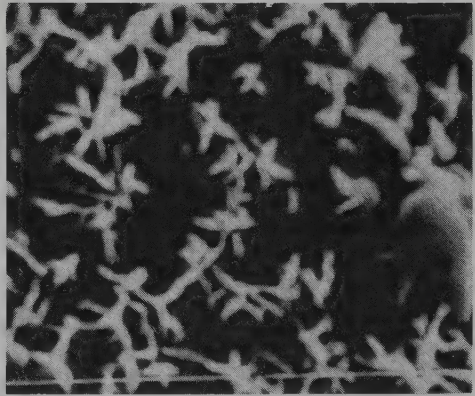
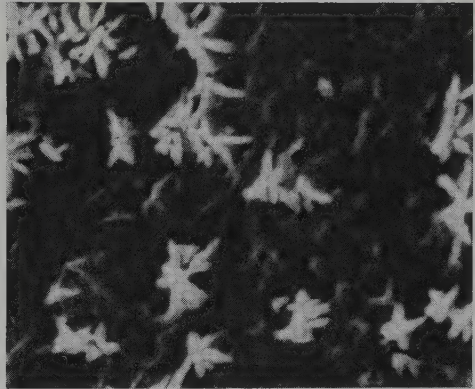
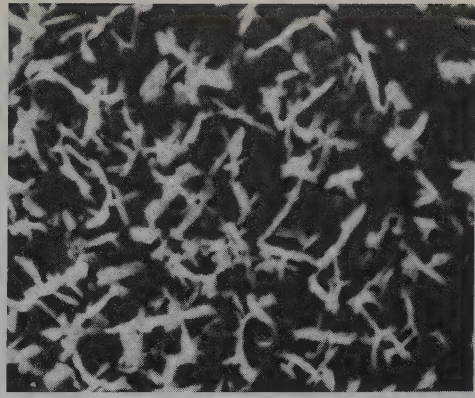
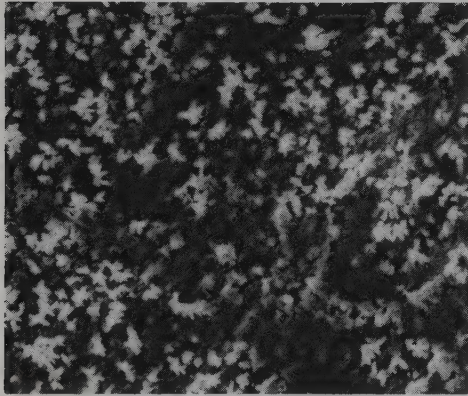
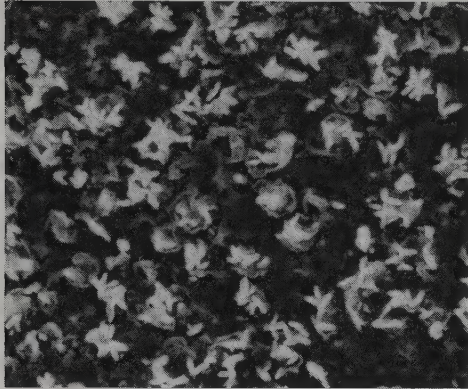
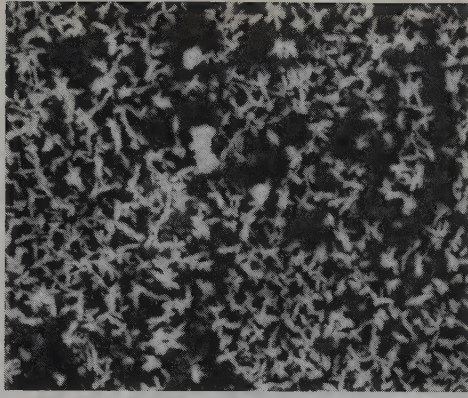


FIGURE 5.a. Epicuticular waxes on the upper epidermis of *Ueratonnia siliqua* grown under different light intensities, at two magnifications. From left to right 100, 80, 50, 10% full light.

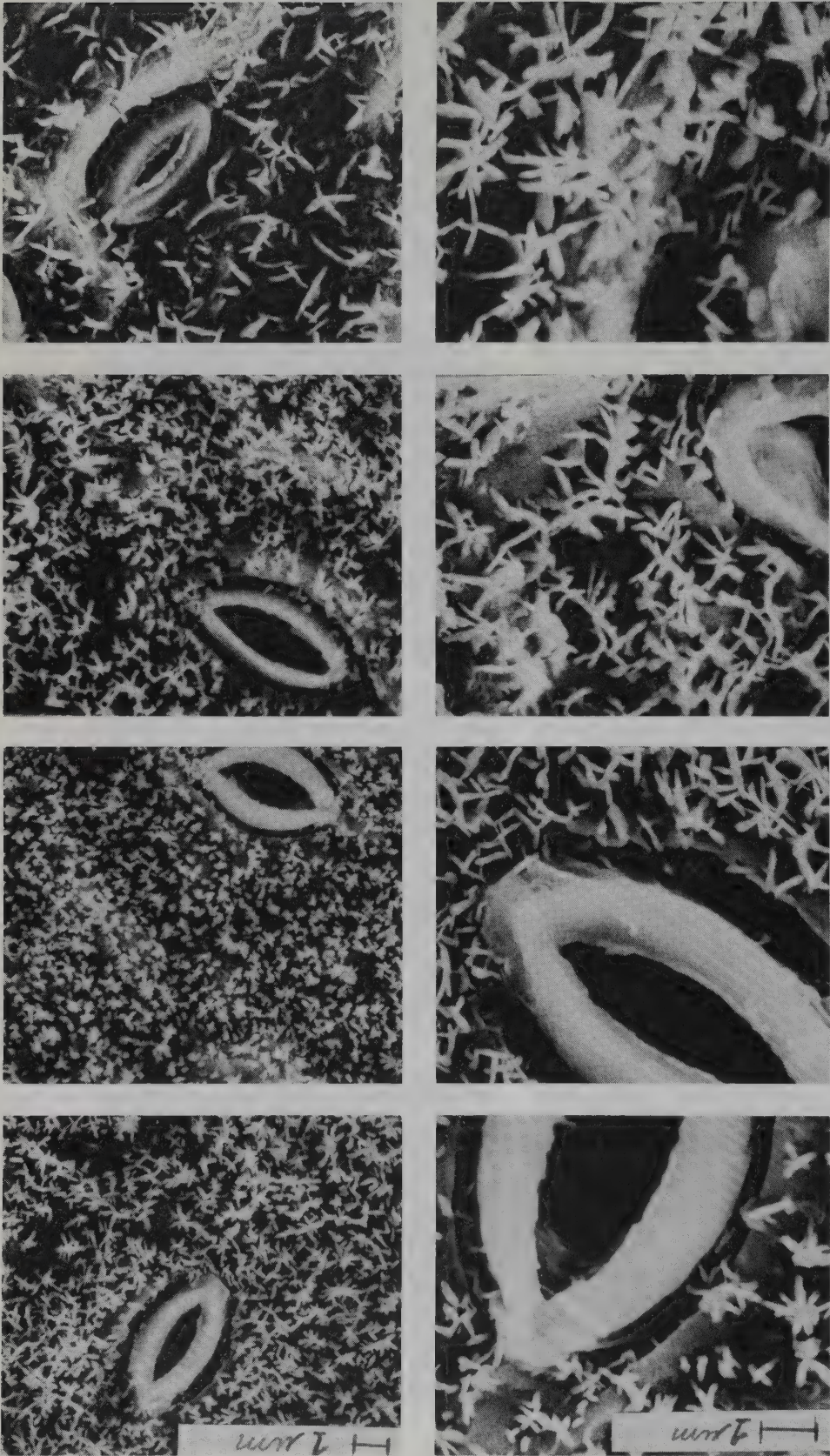


FIGURE 5.b. Epicuticular waxes on the lower epidermis of Ceratonia siliqua grown under different light intensities, at two magnifications. From left to right 100, 80, 50 10% full light.

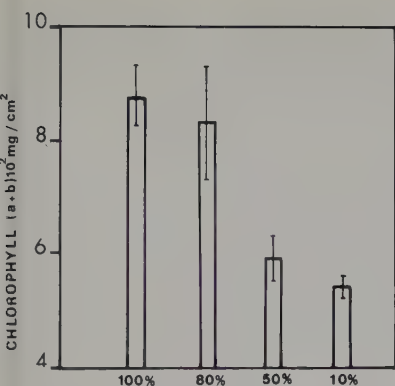


FIGURE 6 Chlorophyll content of mature leaves of *Ceratonia siliqua* grown at 100, 80, 50 and 10% full light.

performed only on the upper surface of leaves. Plants were kept under darkness for 24 hours and then the lower epidermis of pairs of detached leaflets was coated with melted parafin just before the measurement. Transpirational water loss was then measured over 20 minutes period. The results are presented in Table II. Although the variability was great, it seems that higher resistance is not necessarily associated with thick cuticles. On the contrary there is a tendency to find higher resistances in plants with thinner cuticles grown under low light regime.

TABLE I. Chlorophyll content in leaves of *Ceratonia siliqua* grown at different light intensities.

Light %	Chlor. (a+b) (mg / cm ²) x 10 ²	Chlor. (a+b) (mg/g leaf fresh weight)	Chlor. (a/b)
100	8.76	10.96	3.33
80	8.28	11.48	2.87
50	5.88	14.76	3.62
10	5.40	19.52	3.15

TABLE II. Cuticular resistance of upper epidermis to water vapour (rc) of *Ceratonia siliqua* leaves grown at different levels of illumination.

Light Treatment (%)	rc (s cm ⁻¹)
100	163 245
80	199
50	223 387
10	401

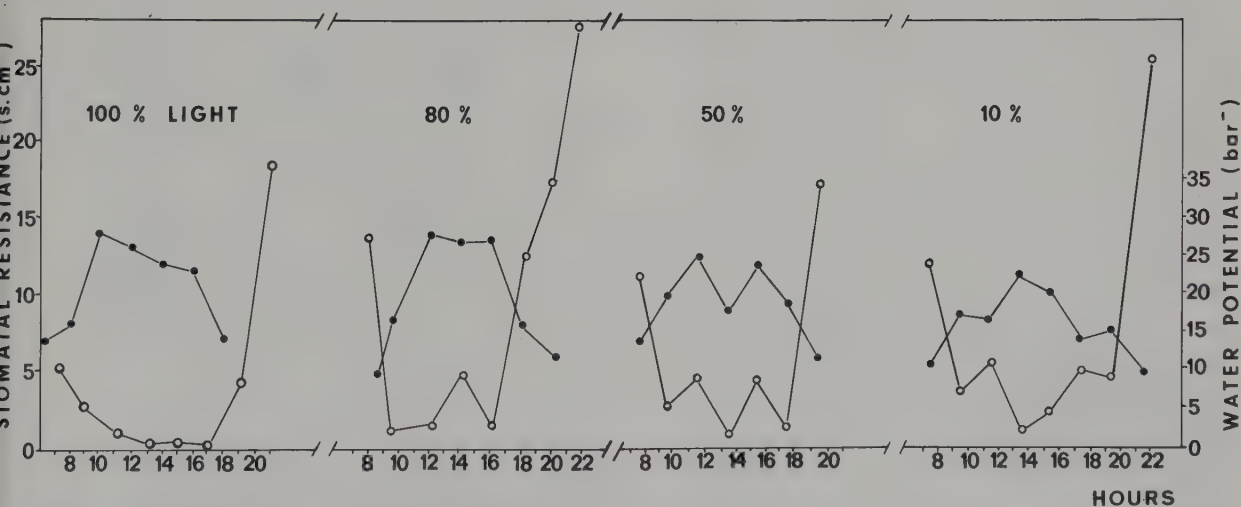


FIGURE 7. Daily course of leaf water potential and resistance to water vapour diffusion of *Ceratonia siliqua* grown at four levels of light intensity.

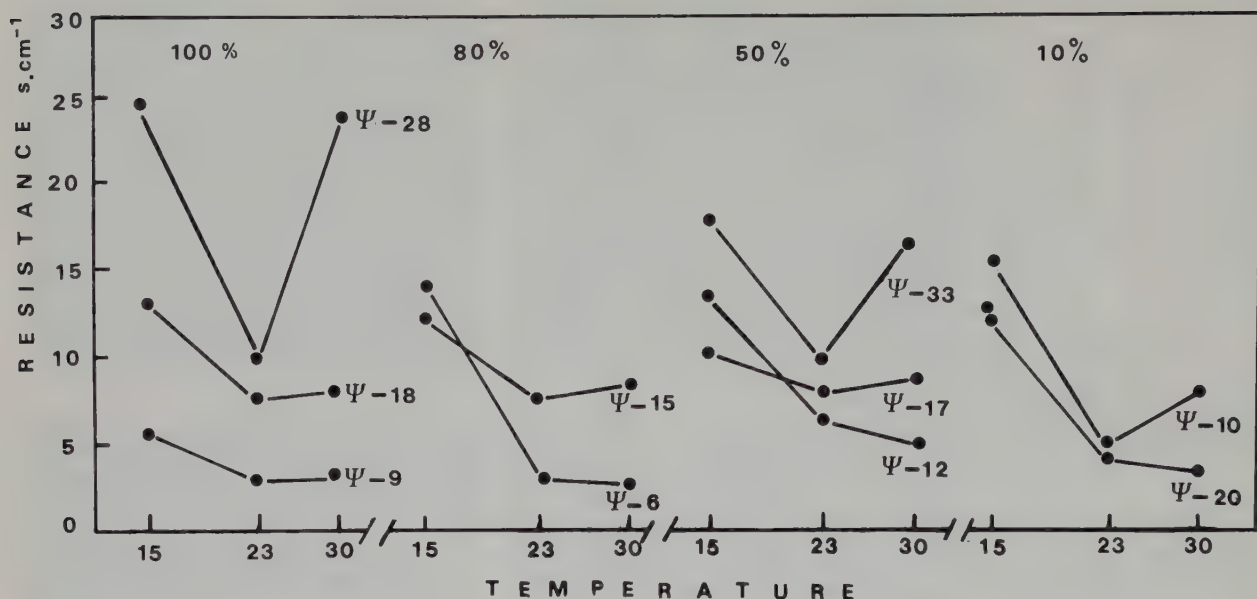


FIGURE 8. Resistance to water vapour diffusion of different irradiance levels grown leaves of *Ceratonia siliqua* as dependent of temperature and water potential.

3.3. Growth analysis

3.3.1. Hydromorphological parameters.

Data shown in Fig. 9 were obtained after 7 months in culture and were determined using leaf discs collected from four leaflets from the 4th and 5th nodes leaves. Five plants of each treatment were analysed. Results show that a marked decrease of sclerophylly is obtained when the light available during leaf morphogenesis decreases.

3.3.2. Growth analysis. Data obtained after 7 and 9 months of plant growth are shown in Table III. From the plants shown in Fig. 10 it is evident that general biomass production is strongly reduced in plants of 50% and 10% light regime. However, some growth parameters are not adversely affected when light is reduced up to 50%. On the other hand, it is evident that the regime of 10% light is not adequate for prolonged growth of *Ceratonia*. For the period analysed, June 12 to August 8, the plants under this regime shows a negative value for relative growth rate (RGR), (Kvet et al., 1971).

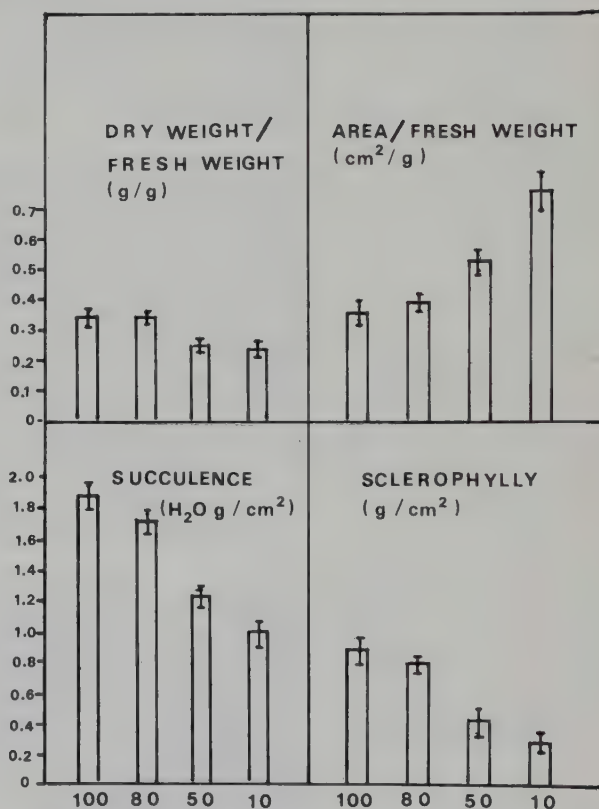


FIGURE 9. Hydromorphological indexes of *Ceratonia siliqua*.

TABLE III. Growth analysis of *Ceratonia siliqua* grown under different light intensities.

Light %	Roots	Dry Weight			Shoot/Root	Leaf Area	Specific Leaf Area	Leaf Area Ratio	Net Assim. Rate	Relative Growth Rate
	(g)	(g)	(g)	(g)		(cm ²)	(g cm ⁻²) x 10 ²	(cm ² g ⁻¹) x 10 ⁴	(g cm ⁻² d ⁻¹) x 10 ⁴	(g g ⁻¹ d ⁻¹) x 10 ³
a) 100	2.35	0.34	3.90	6.68	1.84	276.3	1.41	42.36		
80	3.02	0.53	4.16	7.71	1.55	351.3	1.18	46.57		
50	1.41	0.39	2.33	4.13	1.93	394.6	0.59	95.54		
10	0.58	0.25	1.22	2.05	2.55	276.1	0.44	134.69		
b) 100	3.91	1.12	5.98	11.01	1.82	508.4	1.18	46.18	1.96	8.77
80	4.59	0.99	5.72	11.30	1.46	529.4	1.08	46.86	1.45	6.66
50	3.17	1.39	5.00	9.56	2.01	747.1	0.67	78.15	1.73	14.74
10	0.46	0.32	1.05	1.83	2.98	268.1	0.38	146.51	-14.18	-1.93

a) Measurements done 12 June 1980

b) Measurements done 8 August 1980

Specific leaf area - W/A. Leaf area ratio (LAR) - A/W. Net assimilation rate (NAR) - 1/A.dW/dt.

Relative growth ratio (RGR) - LAR x NAR. From Kvet et al., 1971.

The shoot-root ratio increases for the plants grown under low light indicating that carbon allocation follows a different pattern from plants grown under more strong light.

4. DISCUSSION

As a consequence of their growth by apical meristems higher plants can have a high potential phenotypic plasticity. The continuous serial production of new organs means that the capacity to respond developmentally to environmental influences is present throughout life. It is apparent that these responses may or may not be adaptative (Heslop-Harrison, 1964). Although is not possible to conclude from anatomical structures alone the adaptative advantages of distinct features, several authors have shown that relations between structure and habitat of evergreen sclerophylls exist (Kumerov, 1973). Developmental flexibility and phenotypical plasticity of mediterranean plants like *Ceratonia* are only poorly known. It may be rewarding to obtain a better understanding of the phenology of plants which have been selected to support quite drastic changes in water availability and

FIGURE 10. *Ceratonia siliqua* plants grown for 7 months in 100, 50 and 10% light intensity.

temperature ranges that characterize mediterranean areas and other arid lands. In fact such information can be helpful not only for better understanding of the adaptative mechanisms of natural vegetation to such environments but also for the optimization of crop management under mediterranean climatic conditions.

In natural stands of Ceratonia the particular environment for seedling development may be limited by light intensity under canopy. For this reason we have experimented with very low light growth regimes (10% full light) for the present study. It is clear that although under this light regime Ceratonia growth can proceed at a slow rate the root system is extremely weak as revealed by the shoot to root ratio, which was nearly two-fold higher then under high light intensity. In this respect the plants as developmental strategy similar to that observed in Quercus spp. (Phares, 1971 and Catarino unpublished). However, at least in the seedling stage several Quercus spp. analyzed up to now show that the carbon apportionment to root system is more efficient than in Ceratonia. In fact Ceratonia (100%) has a shoot to root ratio of 1.84 (see Table III) and Quercus only 0.8 (Phares, 1971, Table I pp. 670). Our results revealed that Ceratonia seedlings and young plants are suited for experiments for viewing the acclimations of plants for land management and reforestation. We think that our results bring a better understanding of the development of the Ceratonia canopy structure and composition. The observed leaf plasticity may help bring better approaches for Ceratonia crown modeling either in natural or in crop stands (Correia et al., 1980) as the photosynthetic capacity of this plant depends on the total amount of sun and shade leaves. The development of sclerophylly under high light, the cuticle and epicuticular wax development and the effect of these on leaf functions merit further investigation (Moreira, 1980). Our scanning electron microscope pictures of epicuticular waxes are very similar to the ones obtained in the same material by Nunes and Linskens (1980). There are recent claims that such forms may be

artifacts due to sample preparations for electron microscopy (Rentschler, 1979).

Regarding the production of plants for field transplantation, we conclude that for production of strong root systems more suitable to supporting the plant during the transplantation shock, a high level of irradiance is advantageous.

Furthermore high light grown plants are also capable of better photosynthetic activity since both higher chlorophyll concentration in the leaves and low stomatal resistance are found in those plants. Plants grow at 100 and 80% light under abundant soil moisture exhibit very high leaf conductance to water vapour. This in turn allows for a high rate photosynthesis and consequently a high water-use efficiency, low T/P ratio (Ehleringer et al., 1979).

Regarding the plants grow at low light intensity for use in dry and warm environments, the high leaf resistances and associated increases of leaf temperature can be expected to become critical and such plants may be damage by overheating (Moreira et al., 1980). Induction of strong sclerophylly and thick and reflective cuticular layers for efficient protection against overheating seems to be advantageous for production of Ceratonia plant material for transplantation uses.

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LEAF LONGEVITY IN MEDITERRANEAN EVERGREEN SCLEROPHYLLS

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1. INTRODUCTION

Hoffmann (1878) made direct observations on the leaf longevity of six dicotyledonous evergreen species growing in the Botanical Garden, at Giesen, Germany. Among these species were *Olea europaea* and *Laurus nobilis*, for which he found a leaf life times of 13-26 and 17-53 months respectively.

Kraus (1880) claimed that the leaf longevity found by Hoffmann did not necessarily represent that found in nature. Kraus investigated the leaf duration of many gymnospermous and dicotyledonous evergreen species growing under natural conditions in different regions of Italy. He determined the shoot age of each in years and checked the presence or absence of leaves on them. Among the species he investigated, were the following Mediterranean evergreen sclerophylls for which he found the leaf longevity in years indicated in parenthesis: *Arbutus andrachne* (1 year), *Nerium oleander* (1 or 2), *Phillyrea angustifolia* (1 or 2), *Ceratoniasiliqua* (1 or 2), *Olea europaea* (2 or 3), *Arbutus unedo* (1 or 2), *Rhamnus alaternus* (1 or 2), *Laurus nobilis* (1, 2, 4 or 5), *Quercus ilex* (1 to 4) and *Pistacia lentiscus* (2 to 3 years). These early reports are among the few which exist in the literature on the leaf longevity of Mediterranean sclerophylls. There is also a lack of information on the physiology of leaf longevity, both generally and especially for Mediterranean evergreen sclerophylls. The available data are scarce and the views contradictory (Molisch, 1929, Wagermann, 1965, Steinhübel, 1967)*

*The paper on "Leaf turnover rates of *Adenostoma fasciculatum* (Rosaceae)" by W.M.Jow et al. in *Amer.J.Bot.* 67(2), 256-261, 1980 appeared after we completed our paper.

2. MATERIAL AND METHODS

Leaf longevity was studied in *Quercus coccifera* L., *Pistacia lentiscus* L., *Arbutus andrachne* L., *Arbutus unedo* L., *Myrtus communis* L., *Olea europaea* L., var. *oleaster* (Hoffm. u. Link) growing in the wild in Malakasa, 30 km north of Athens, and in *Ceratoniasiliqua* L. planted in the eastern suburb of Athens (Monastery of Kaisariani). In each of two plants of these species, four young shoots were selected in March 30th, 1976. In each shoot the leaf emergence and the leaf fall was followed until all leaves had fallen, i.e. until October, 1978. During this period we made 12 observations on the dates listed below: 30.3.76, 17.5.76, 8.7.76, 10.10.76, 4.1.77, 10.4.77, 10.7.77, 8.10.77, 2.3.78, 5.5.78, 10.7.78 and 2.10.78. To calculate the longevity of each leaf, we considered as the date of its appearance or its fall the middle of the time interval between the date we noticed the appearance or fall and the previous observation. This means that our method allows a maximum error of 3 months. Although, as mentioned, we selected eight shoots for each species, the data presented are means of five shoots, for which no indication for damage from insect or other animals etc. was noticed.

3. RESULTS

Leaf appearance (Table I) followed a similar pattern in the seven species studied: at the end of March, when our observations began, the shoots had 10-22% of the total leaves they would form. This percentage rose to 55-80% at the beginning of May and reached the maximum value sometimes before (or on) July 10th. In contrast, leaf fall kinetics differentiated the seven species into two groups. One with shorter (*P.lentiscus*, *A.andrachne*, *A.unedo* and *Q.coccifera*) and another with longer (*C.siliqua*, *M.communis* and *O.europaea* var. *oleaster*) leaf durations. In the first group leaf fall was first noticed

TABLE 1. Leaf appearance and leaf fall kinetics in seven Mediterranean evergreen sclerophylls. The first row of numbers represent leaves/shoot and are the means for five shoots. Relative number (%) for leaves/shoot are also given.

Date of observation	Species	30.3.76	17.5.76	8.7.76	10.10.76	4.1.77	10.4.77	10.7.77	8.10.77	2.3.78	5.5.78	10.7.78	2.10.78
	<i>Arbutus</i>	4.2	17.6	22.6	22.6	21.4	14.4	7.8	3.6	0.6			
	<i>andrachne</i>	(18.6)	(77.8)	(100)	(100)	(94.7)	(63.7)	(34.5)	(15.9)	(2.6)			
	<i>Arbutus</i>	5.2	19.2	26.4	26.4	26.4	24.2	13.0	5.2	0.4			
	<i>unedo</i>	(19.7)	(72.7)	(100)	(100)	(100)	(91.7)	(49.2)	(19.7)	(1.5)			
	<i>Quercus</i>	2.4	7.2	11.6	11.6	11.6	9.0	4.2	1.6	0.0			
	<i>coccifera</i>	(20.6)	(62.0)	(100)	(100)	(100)	(77.6)	(36.2)	(13.8)	(0)			
	<i>Pistacia</i>	3.0	7.4	13.4	13.4	11.8	6.0	2.6	0.6	0.0			
	<i>lentiscus</i>	(22.4)	(55.2)	(100)	(100)	(88.1)	(44.8)	(19.4)	(4.5)	(0)			
	<i>Ceratonia</i>	2.4	10.8	14.0	14.0	14.0	14.0	13.4	13.2	9.2	5.4	3.0	0.6
	<i>siliqua</i>	(17.2)	(77.2)	(100)	(100)	(100)	(100)	(95.7)	(94.3)	(65.7)	(38.6)	(21.4)	(4.3)
	<i>Myrtus</i>	2.8	19.2	25.2	25.2	25.2	25.2	25.2	22.8	15.6	6.8	1.6	0.0
	<i>communis</i>	(11.1)	(76.2)	(100)	(100)	(100)	(100)	(100)	(90.5)	(61.9)	(27.0)	(6.3)	(0)
	<i>Olea</i>	2.8	11.2	14.8	14.8	14.8	14.8	14.8	14.0	8.4	5.4	2.6	0.2
	<i>europaea</i>	(18.9)	(75.7)	(100)	(100)	(100)	(100)	(100)	(94.6)	(56.7)	(36.5)	(17.6)	(1.3)

ed in January (*P.lentiscus*, *A.andrachne*) or April (*A.unedo*, *Q.coccifera*) 1977. Until July 10th 1977 50-80% of the leaves had fallen, while leaves which fell during the summer (from July 10th to October 8th) constituted 15-30%. Leaf fall was practically completed by October 1977. In the second group we noticed leaf fall began (with the possible exception of *C.siliqua*) in October, 1977. From October, 1977 to March 2nd 1978 30-40% of the leaves were lost. A higher leaf loss (40-55%) was noticed during the growth season (from 2.3.78 - 10.7.78). The remaining leaves (less than 20%) fell during the summer period. Leaf longevity varies considerably within the same shoot, the general trend being that the top leaves show a longer life time than the ones appearing first. Thus, in *A.andrachne* leaf longevity varies between 7.9 and 18.3 months, in *A.unedo* and *Q.coccifera* between 10.9 and 18.3

months, in *P.lentiscus* between 7.9 and 15.7 months (Table 2). Mean values for leaf longevity, calculated from the data of Table 1, are as follow for the four species respectively: 12.6, 15.1, 13.8 and 11.3 months. Leaf duration in *C.siliqua* varied between 16.8 and 26.7 months, in *M.communis* between 17.9 and 25.9 and in *O.europaea* var. *oleaster* between 19.4 and 26.7 months. Mean values for the three species of the second group are 23.6, 22.5 and 23.4 respectively.

4. DISCUSSION

Only old and uncertain data exist concerning the leaf longevity in Mediterranean evergreen sclerophylls (Hoffmann 1878, Kraus 1880). Attempts to analyse the significance of this phenomenon are based on unrelated data (Molisch, 1929, Wangermann 1965, Steinhübel 1967). Our data refer only to the spring leaves of plants growing in a single locality.

1. INTRODUCTION

Reviewing the literature on the leaf anatomy of the sclerophylls, Kummerow (1973) summarizes that water stress, high light intensities and nitrogen deficiency are the reasons for a low surface to volume ratio. This surface reduction is further characterized by modifications of the leaf anatomy such as smaller cell size, higher stomatal frequency, thicker cell walls, more veins per surface unit area, a thick cuticle, strong mechanical tissue, more developed palisade parenchyma etc. Concerning the Mediterranean evergreen sclerophylls in particular, it is at present rather generally accepted (Mooney, Dunn 1976, Mooney et al. 1974, Persons, Moldenke 1975, Parsons 1976, Dunn et al. 1976) that these leaf anatomical features constitute "adaptive strategies" employed on purpose to evade the drought stress of the mediterranean climate.

Palaeobotanical records (Axelrod 1973, Raven, Axelrod 1978) suggest that the evergreen sclerophylls are older than mediterranean climate, which does not support the view that these species evolved responding to this climate.

Furthermore the palaeobotanical records suggest that the Northern Hemisphere mediterranean floras have been evolving since Cretaceous time in the ecotone between temperate and tropical forest, accumulating derivatives from both temperate and tropical predecessors, opposite to what happened to the Southern Hemisphere mediterranean floras which they come almost entirely from the tropics (Raven 1973). Thus many of the genera common to the Mediterranean basin and to California were probably evolved from temperate ancestors of the Arcto-Tertiary Geoflora, while other taxa come from the Madro-Tertiary (California) or the Mediterranean-Tertiary (Mediterranean basin) geoflora. One should then refer to data expressing the leaf

sensitivity of the mediterranean evergreen sclerophylls to low temperatures (Larcher 1970, 1973), which varies considerably among various species while in general it seems that their ability to survive the direct action of very low temperatures without suffering permanent damage is limited (Larcher 1973). Distribution data of the evergreen sclerophylls along winter cold gradients (Mitrakos 1980), are in agreement with these data.

On the basis of the literature cited above we find it interesting to examine how the leaf anatomical features vary or converge within the evergreen sclerophylls. In this paper quantitative data are reported concerning leaf size and leaf anatomy on a microscopic level for seven species.

2. MATERIALS AND METHODS

A typical macchie site 37 km North of Athens was selected, and mature leaves from six species (*Arbutus andrachne*, L. *A.unedo* L. *Olea europaea* L. var. *oleaster* Hoffm. and Link, *Pistacia lentiscus* L. *Phillyrea media* L. and *Quercus coccifera* L.) were collected during the last days of August 1979. Leaves of *Ceratonia siliqua* L., a species naturally not reaching that north, were collected from trees grown in the Eastern suburbs of Athens.

Ten mature leaves from each one of three plants for every species were cut in small pieces (1x1 mm) fixed in Glutaraldehyde 3% in phosphate buffer, postfixed with Osmium tetroxide 1%, dehydrated in graded alcohol series and embedded in resin (Durcupan ACM-Fluka). Semithin sections were obtained on an LKB ultramicrotome and stained with toluidene blue. The presented figures came out of observations from 60 leaf sections for each species taken at random.

For the localization of polyphenols, free hand sections were subjected to various histochemical reagents. The general reagents used were: a) 10% Ferric sul-

fate (Chafe, Durzan 1973), b) 2% Sodium acetate (Haas, Hill 1921), c) 3% Ammonium dichromate (Haas, Hill 1921), d) 2% Uranyl acetate (Haas and Hill 1921). In addition, the following specific reagents were applied: e) The nitrous acid reagent to detect the nitroso deviratives of o-dihydroxyphenols. Equal volumes of 10% NaNO_2 , 20% urea and 10% acetic acid were added in succession to the sections on the slide and after 3 minutes two volumes of 2N NaOH followed (Reeve 1959), f) The aniline iodate reagent to detect the aniline addition products of quinones derived from phenols. This reagent consists of 0.5 ml aniline, 5 ml distirled water and 20 ml of 0,5 M NaCO_3 (Endress, Thompson 1975), g) The DMB reagent, which consists of equal volumes of 18% HCl and 1% 3,4, dimethoxybenzaldehyde and is used for the detection of the flavonoid phenolic precursors of condensed tannins forming a brilliant red reaction product (Mace, Howell 1974).

Sudan Black B for indentification of lipids and starch in sections of epoxy embedded tissues was applied according to Bronner (1975). Lipids were visualized as black droplets while starch remained unstained against a dark blue background.

3. RESULTS

Leaf size (Fig.1) length, breadth and thickness were measured (for the composite leaves of *C.siliqua* and *P.lentiscus* the leaflet dimensions were considered). Leaf surface values were calculated by drawing a " mean size" leaf on a graph paper, adopting the mean values of length and breadth and the outline curvatures from a real leaf of the same size. The number of the enclosed 1 mm² squares is the leaf surface. Length and breadth (and surface consequently) vary considerably in the species studied. The ratio of the shortest (*P.media*) to the longest (*A.andrachne*) leaf is 1:3.70 while the ratio of the narrower (*O.europea* var. oleaster) to the wider one (*A.andrachne*) is 1:9.2. *A.andrachne* has the largest leaves (ca. 2610 mm²) which is 24 times larger than the leaves of *O.eu-*



FIGURE 1. Leaf size and shape of the seven evergreens studied L=length, B=breadth, S=surface, T=thickness in mm. For L and B n=300, for T= n=60.

ropea var.oleaster with the smaller ones (ca. 110 mm²) Both *Arbutus* species (*Ericaceae*) have relatively large leaves and both species of *Oleaceae* family small ones. The leaves of *Q.coccifera* (ca. 190 mm²) as well as the leaflets of *P.lentiscus* (ca. 200 mm²) are small while the leaflets of *C.siliqua* are characterized by intermediate size (ca. 800 mm²). Leaf thickness varies between different species considerably less than the other two dimensions do, yet leaves of *A.andrachne* are 80% thicker than the leaves of *P.media*. Length, breadth and thickness do not correlate between each other in the species studied. Having measured the thickness of the leaf and that of both upper and lower epidermis, we can calculate the mesophyll thickness. Thus, we were able to examine closer the two elements contributing to leaf thickness i.e. the protective tissues (upper and lower epidermis) and the photosynthetically active tissue (the mesophyll). Upper plus lower epidermis constitute about 12% of the leaf thickness. Extreme cases are *C.siliqua* (19%) and *O.europea* var. oleaster (7%). In the latter species stomatal frequency, compared to that of others (i.c. *C.siliqua*) is high. Evidently the protective role of the epidermis in

this species is reinforced by other anatomical features (i.e. thick outer walls, hair cover etc.). On the contrary *C.siliqua* shows thin outer walls and cuticle, no hair etc. In all species upper and lower epidermal tissues do not vary on the basis of a general pattern and commonly they assume intermediate values. The relative thickness of the photosynthetically active tissue does not vary considerably (81-91% of the leaf thickness) but the absolute thickness of the two extremes make a ratio of 1:1.6. More interesting is the stru-

detect the presence of tannins. The two Oleaceae species reacted negatively. The positive reaction of the other four species is differentiated (Table II) as follows: In both *Arbutus* species and *P.lentiscus* tannins are located in the mesophyll (both in palisade and spongy parenchyma) and in the epidermal cells. In *C.siliqua* the cells of both the upper and the lower epidermis and those of the bundle sheaths react strongly the reaction becoming weaker deep in the mesophyll. In *Q.coccifera* there is an extremely wide distribution of tannins in all tissues.

TABLE I. Quantitative histological data for the leaves of the seven evergreen species.

n= 60	e p i d e r m i s							m e s o p h y l l					m e c h . t i s s u e		
	thickness (μm)		cell walls and cuticle (μm)				stomatal frequency	hair	compactness	size of palisade tissue cells (μm)	portion % of palisade tissue cells	number of layers	type	colenchyma	sclerenchyma
	upper surface	lower surface	upper surface		lower surface										
			outer walls	cuticle	outer walls	cuticle									
<i>Arbutus andrachne</i>	31±4	20±4	11±3	3	5±2	2	155	%	●●	74±19	45	3	h	●	■
<i>Arbutus unedo</i>	37±6	32±6	13±5	4	11±4	3	190	%	●	75±12	42	2	h	●	■
<i>Ceratonia siliqua</i>	40±7	21±6	3±3	1	2±3	1	224	%	●●	54±26	34	2	h	●	■
<i>Olea europea</i>	20±3	15±3	9±2	1	4±1	1	386	%	●	57±25	36	3	h	●	■ ■
<i>Pistacia lentiscus</i>	28±5	22±6	10±2	2	8±2	2	234	%	●	69±30	39	2	h	● ●	■
<i>Phillyrea media</i>	19±3	13±2	12±2	1	7±1	1	474	%	●●	40±9	40	3	h	●	■ ■
<i>Quercus s coddii</i>	19±2	17±3	7±2	2	4±2	2	228	%	●●	44±14	49	3	h	● ●	■ ■

cture of the palisade tissue. It constitutes, in the different species, 34-49% of the mesophyll thickness, but in some species it consists of three while in others of two layers. The mean length of palisade cells is between 40 μm (*P.media*) and 75 μmm(*A.unedo*). No correlation exists between the number of palisade cell layers and the mean length of the palisade cells. Thus the absolute thickness of the palisade tissue varies between 90 μm (*C.siliqua*) and 228 μm (*A.andrachne*). The mesophyll compactness varies rather irregularly, the presence of colenchyma is common, but sclerenchyma though existing in all species is abundant only in the leaves of the two Oleaceae species.

In free-hand section tests with 10% ferric sulfate, 2% sodium acetate, 3% ammonium dichromate and 2% uranyl acetate were employed in order to

TABLE II. Tannin occurrence in leaf tissues of the seven evergreens studied. ○ no reaction, ● weak reaction, ● strong reaction, ●● very strong reaction.

	A.andrachne	A.unedo	C.siliqua	P.lentiscus	O.europea	P.media	Q.coccifera
upper epidermis	●	●	●●	●	○	○	●
palisade 1 st layer	●●	●●	●	●●	○	○	●
palisade 2 nd layer	●	●	●	●●	○	○	●
palisade 3 rd layer	●	—	—	—	○	○	●
spongy parenchyma	●●	●●	●	●●	○	○	●
lower epidermis	●	●	●●	●	○	○	●

Effort was also made to detect precursors of the condensed tannins. Applying the DMB test the results are in agreement with those of the general tests though by this test *Q.coccifera* seems to react negatively.

Lipids were detected in the vacuole and plastids,

mostly of the palisade tissue cells of all seven species. With the exception of *P.media* and *P.lentiscus* lipid droplets are small while in *A.andrachne* and *A.unedo* they are large. In *Q.coccifera* droplets are large too and particularly numerous. In the plastids of all species small starch granules were detected.

3. DISCUSSION

Although everyone accepts Grisebach's opinion concerning the physiognomic similarity of the sclerophyllous vegetation in areas with mediterranean climate (Raven 1973), we agree with Johnson (1973) who stated that the study of the evolutionary phenomenon known as vegetation convergence is still in a relatively early and descriptive phase and has been examined at a species population level. We, focus our interest not on convergence of "higher units" or "ecosystems" as it is interestingly done by Johnson (1973), but to the microscopical level of one single organ: the leaf. In as much as we are at present investigating the fine structure of these leaves, we consider the data presented in this paper as preliminary. We are also aware of the fact that the seven species examined constitute less than 50% of the sclerophyllous trees or shrubs growing in Greece. Considering climate vegetation relationship in mediterranean-climate countries one recognizes not only the sclerophyll convergence, but also geophyte (Schimper 1898) as well as an annual plant convergence (Raven 1973). The study of the mediterranean woody plant convergence must not be restricted only to the leaf structure but also to other structural features, such as the deep root system etc. On the other hand, we know, at least since Grisebach, that sclerophyllous trees or shrubs are not restricted only to mediterranean zones, but also occur in the tropics as well as in arctic areas. As far as we know no one has found a clear cut difference between the mediterranean plant leaf structure and the hard leaves of plants occurring in other climates

(Pyykko 1966). Trying to understand the climatic causes of the mediterranean hard leaves one first has to recognize that the mediterranean evergreen sclerophylls are older than the mediterranean climate (see excellent reviews by Axelrod 1973 and Raven 1973). By the Miocene time most sclerophylls were similar to the modern species and lived during the subsequent 25 million years in a climate with adequate summer rain fall and only in the last one million years under the mediterranean climate. Thus, it is difficult to know at present under which conditions these leaves were shaped, more over it is also both difficult and interesting to know when and why the "sclero" feature and the "evergreen" habit were combined in these leaves. These questions stress the need for a closer and deeper investigation of this fascinating phenomenon.

Leaf size, (expressed as surface) does not converge in the seven species studied since the ratio of the large (*A.andrachne*) to the smaller (*P.media*) leaves is about 24. Four species (*O.europea*, *P.media*, *Q.coccifera* and *P.lentiscus*) show leaf size smaller than 200 mm² while the two *Arbutus* species are larger than 1300 mm². In *Ceratonia* they have intermediate on size (800 mm). Leaf thickness does not vary as much as the leaf surface, but is difficult to consider it convergence, before a comparison with the corresponding thickness of the leaves in mesophytes is made. At any rate, these data do not support the view that the decrease of the surface to volume ratio is accompanied by modifications of leaf anatomy.

Cell thickness of the epidermis varies less than that of the leaf and mesophyll thickness. In contrast, outer wall thickness in the two sides of the epidermis make a ratio in the two extreme cases equal to about 3.6. Some species show thick epidermal cells with thick outer walls (the two *Arbutus* species). Others (*Ceratonia*) show thick epidermal cells but thin outer walls. Moderate cell and wall thickness is shown in the species *O.europeae* var. *oleaster*, *P.lentiscus*, *P.media* and *Q.coccifera*. Stomatal frequency seems to be a family feature:

The two Ericaceae have the lower frequencies (155, 190), the two Oleaceae the higher ones (386, 474).

Ceratonia epidermis, combines thick epidermal cells, thin outer walls and low stomatal frequency. It is a drought resistant species. The *Arbutus* species combine a moderate thickness of epidermal cells and their outer walls with a low stomatal frequency. Both are less drought resistant than *Ceratonia siliqua*. *Phillyrea* and *Olea*, show thin epidermal cells, moderate thickness of outer walls and a high stomatal frequency. *Olea* is drought resistant, but the presence of a dense hair cover may also contribute to this. One could say that there exists a physiological convergence, i.e. control of transpiration via epidermis, but this is obtained by different structure and/or combination of structures. The presence of tannins in the epidermis of most of the species, possibly contributes to the protective role of this tissue not only against drought but also against herbivores.

The lack of physiological information (e.g. photosynthesis temperature dependence) make difficult to understand if there exists convergence or diversity in the differentiation of the mesophyll. The morphological features reported in this paper, in any case, show a convergence in what concerns the relative thickness of the palisade tissue, being about 45% of the mesophyll thickness. Again one should compare these figures with the corresponding ones of mesophyte leaves.

In closing this discussion we would like to emphasize that biological convergence needs to be further investigated both in microscopical and ultrastructural level.

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1. INTRODUCTION

The Cistaceae, a family with resinous plants, namely *Cistus ladaniferus* and *Cistus monspeliensis*, is widely distributed in Portuguese Mediterranean habits.

Leaves and stems of these two species, secrete a fragrant oleoresin containing a mixture of terpenoids and flavonoids (Cocker, Harsall, 1956; Tabacik, Bard, 1971; Königs, Gülz, 1974).

There are several purposes for studying the biosynthesis of this resin. The economical interest of some components of the exudate, which are used as fixatives in perfumes industry and the possible ecological significance of resins. In addition, little is known about the biosynthesis and transport of these compounds within the cell.

Finally, in areas with degraded soils, where *Cistus* plants are the dominant shrubs, the cost of soil improvement would be so expensive, that the rate of interest to the capital employed, would be higher than the forecasted income from such project. In such cases, soil productivity would be so low that it would be better to find out an adequate use for the dominant plants - the Cistaceae. For these reasons, every background information concerning *Cistus* must be very useful (Katznelson, 1977).

Reports on the ultrastructure of trichomes secreting resins of some other species, have been published (Dell, McComb, 1974, 1975, 1977; Thomson *et al.* 1979). The aim of our paper is to describe some inframicroscopic aspects of the glandular trichomes in *Cistus monspeliensis* and their relation with resin production.

2. PROCEDURE

2.1. Material and methods

2.1.1 Plant material

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Plants of *Cistus monspeliensis* were collected at the SW region of Cabo Espichel, western Portugal, and kept, during the transport, under moist conditions, in plastic bags for 1-2 hours.

2.1.2 Light microscopy

Histochemical tests have been performed on fresh material (meristems and leaves) stained with Sudan black B.

Fresh sections were also observed in a Zeiss fluorescence microscope equipped with an HBO 200W mercury arc lamp, as the source of radiation, exciter filters 47 and 53 and barrier filter II. Semi-thin, 0.5 μ m thick, of material prepared as for T.E.M. were stained with Paragon multiple stain and with Sudan black B (Bronner, 1975; Parham, Kauskinen, 1976; Bircham, Brown, 1978).

2.1.3 Electron microscopy

For T.E.M., meristems and segments of young leaves were fixed in 3% glutaraldehyde in 0.15M PIPES buffer pH 8.0 for 1 hour, and post-fixed, for the same period, in 2% OsO₄ buffered to pH 6.8 with PIPES (Salema, Brandão, 1973). Tissues were dehydrated in acetone series and embedded in Epon-Araldite mixture. Ultrathin sections were made on a Porter-Blum, MT-2 ultramicrotome, stained with uranyl acetate, lead citrate and examined in an Hitachi HU-12 electron microscope at 75 KV.

For S.E.M. the material was mounted with electron conductive glue (silver paint), quenched-frozen in liquid nitrogen and observed in a CAMECA scanning electron microscope at 3 or 4 KV.

3. Results

3.1. Light microscopy

3.1.1. Morphology and distribution of the secretory trichomes

In later Spring and Summer, plants of *Cistus* show great amount of resin, in a continuous sheet

of odouriferous varnish over the adaxial surface of leaves and stems. This confers to the leaves adaxial surface a mirror like character.

The resin, an amorphous substance insoluble in water, but soluble in organic solvents as ether and chloroform, occurs as a thick sheet, filling the spaces between the trichomes (Pl. I, fig. 3,8).

In *Cistus monspeliensis* leaves and stems there are two different types of glandular hairs

- a) Capitate trichomes (up to 90 μm) with long stalks two to three cells, and glandular heads with six to eight cells separated by horizontal and parallel walls (Pl. IV, fig. 5a). These trichomes are abundant on the adaxial surface of the leaves, but they are also present on the abaxial one.

- b) Bulbous trichomes, very small (up to 45 μm) with a long stalk cell and a glandular head formed by 2 cells (Pl. V, fig. 1). They are scattered and confined to the abaxial surface of the leaves particularly on the proximity of the midrib. It is very difficult to visualise them, due to their small dimensions and to the covering stellate-tomentose indumentum.

3.2. Fluorescence microscopy

Under ultraviolet light the resin have a green-yellowish autofluorescence. It is possible, by this method, to recognise different steps in capitate trichomes secretory process. The resin is firstly detected in the upper secretory cell of these trichomes (Pl. I, fig. 6) than in the sub-cuticular space where it begins to accumulate. Finally the exudate is released and run down covering the leaves and stems surface filling the spaces between the numerous trichomes (Pl. I, fig. 3,6).

3.3. Histochemical tests

In fresh sections, Sudan black B, show the typical staining for lipids. The exudate is seen in capitate trichome glandular cells and in the sub-cuticular space.

In semi-thin sections stained with Sudan

black B, blue dark spherules are observed in the cytoplasm and vacuoles of glandular cells specially in the capitate trichomes upper cell (Pl. I, fig. 4,5,7,8). Orange brown deposits can be seen in the vacuoles of some epidermal and parenchyma cells (Pl. I, fig. 5,8). Very often the secretory product accumulate in the sub-cuticular space is removed by the conventional fixation methods used for T.E.M. (Pl. I, fig. 7).

3.4. Electron microscopy

3.4.1. Scanning electron microscopy

The scanning electron micrographs show the morphological types of *Cistus monspeliensis* trichomes (Pl. I, fig. 1,2).

3.4.2. Inframicroscopic observations

In the early secretory stage, capitate and bulbous trichomes show glandular head cells with a dense cytoplasm rich in ribosomes, mitochondria, plastids, dictyosomes and E.R.. These cells also present small vacuoles and large nucleus (Pl. II, fig. 1 ; Pl. V, fig. 1).

a) Capitate trichomes

In young trichomes E.R. profiles with a parallel disposition are seen in the proximity of the plasmalemma (Pl. II, fig. 5). Very often the gland cells possess a well developed Golgi apparatus. Dictyosomes have, in medium, five flat cisternae with swollen margins and abundant Golgien vesicles (Pl. II, fig. 2).

With the onset of the secretory phase, the number of mitochondria and plastids greatly increase (Pl. II, fig. 4; Pl. III, fig. 1). The mitochondria present abundant, swollen cristae; plastids with few thylakoids show a dense stroma with osmophilic droplets (Pl. III, fig. 1). Starch granules have never been observed in the plastids. An extensive tubular network of E.R. is observed throughout the cytoplasm in close relation with mitochondria and plastids (Pl. II, fig. 3; Pl. III, fig. 4; Pl. IV, fig. 1,2,3). Frequently, plastids are surrounded by E.R. and, occasionally, connections between the plastidial envelope and the periplastidial E. R. can be seen (Pl. IV, fig. 2,3 arrows). In some cases there is an

intimate association between the membranes in contact. Plastids envelope seems to be formed by three membranes : one corresponding to the inner membrane of the plastid envelope; the second formed by fusion of the outer membrane of plastid envelope with the endoplasmic reticulum membrane in contact; the third one is the E. R. membrane that faces the cytoplasm and conserves the ribosomes (Pl.IV, fig. 2). Electron dense material is present within swollen E.R. profiles (Pl.III, fig.2). Large vacuoles are formed by fusion of small ones (Pl.III, fig.3). Osmiophilic material similar to that one observed in E.R. is seen adherent to the vacuoles to noplast (Pl. III, fig.3). During the fusion of vacuoles, the secretory products coalesce to form large accumulations which eventually fill the vacuoles (Pl. III, fig. 4).

In mature glands the cuticle of terminal cells becomes detached from the microfibrillar layer of the wall (Pl. IV, fig.5a,5b,6). Secretion is accumulated in the sub-cuticular space. Release of exudate occurs by rupture of cuticle (Pl.IV, fig.5c).

In later secretory process, cellular lysis begins in the upper cell following in the others until trichomes death (Pl. IV, fig.5c).

b) Bulbous trichomes

The glandular head cells of these trichomes are typical transfer cells (Pl.V, fig. 1). The characteristic wall ingrowths are organised in a labyrinthiform pattern (Pl.V, fig.4). The plasmalemma presents many infoldings following the cell wall on its whole length.

A dense cytoplasm with abundant organelles particularly mitochondria with well developed cristae, are aligned along the plasmalemma (Pl. V, fig.1,5). Occasionally, they are located between two wall protuberances. In this case, the cytoplasm virtually disappears, allowing the establishment of a close association between the mitochondrial membrane and the plasmalemma infolding (Pl.VI, fig.5).

Cytoplasmic ribosomes usually in clusters, presumably polysomes are seen (Pl.VI, fig.3,4 arrow). R. E. R. profiles, in a parallel arrangement, lie near the plasmalemma and sometimes are in direct contact with it (Pl.VI, fig. 3,4,6, strong arrow). Golgi vesicles and small vacuoles are abundant (Pl. V, fig.2; Pl.VI, fig.1).

In the central region of cell walls between the stalk cell and the adjacent head cell, and between this one and the upper head cell, plasmodesmata are observed (Pl.V, fig. 1,2,4,5).

Osmiophilic droplets can be seen crossing the loose fibrillar cell wall layer (Pl. V, fig.3; Pl.VI fig.1,2,3).

The stalk lateral cell walls are cutinised and adherent to the plasmalemma (Pl. V, fig.1, strong arrow).

4. Discussion

a) Capitate trichomes

The histochemical study and the autofluorescence observed under ultraviolet light reveal the lipophilic character from the exudate. These results are consistent with the chemical analysis of the secretory product. The blue dark deposits observed in the cytoplasm and vacuoles of these trichomes may correspond to oleoresin. The orange brown accumulations in the epidermal and parenchyma cells must be tannins.

As we described the extensive tubular network of E.R. is the main feature in capitate trichome glandular cells. Identical observations have been reported in cells secreting essential oils, flavonoids and other lipid compounds (Schnepf, 1969, 1972; Heinrich 1973; Amelunxen, Arbeiter, 1969; Tsekos, Schnepf 1974; Charrière-Ladreix, 1975; Dell, McComb, 1974, 1977).

Plastids in *Cistus monspeliensis* capitate gland cells possess few thylakoids and are often enveloped by E.R. profiles. This is also a common aspect of other resin secretory trichomes (Wooding, Northcote, 1956; Vasiliev, 1969; Fahn, Evert, 1974; Dell, McComb 1977; Benayoun, Fahn, 1979). Nevertheless, connections between plastids envelope and E.R. have ne

ver been reported, at the best of our knowledge, in resin secreting trichomes. In our case, the presence of osmiophilic material in plastids and in E.R. profiles strongly suggest that these two organelles play an important role in the biosynthesis and secretion of oleoresin. Membranar connections between E.R. and plastids allow us to suppose that the secreted material produced by plastids can be transferred to the periplastidial E.R. and accumulated temporarily in the vacuoles. This does not exclude the role of E. R. in some steps of resin biosynthesis. Similar features have been described and identically interpreted by authors working with duct cells (Mikulska, Zolnierowicz, 1976; Benayoun, Fahn, 1979),

Taking in account our preliminary results on *Cistus monspeliensis* capitate trichomes, we agree with Dell's opinion (1977) on the typical main features of resin secreting cells: 1-plastids with few thylakoids, 2-E.R. particularly well developed. Nevertheless, it is necessary to join, to these features and for trichome cells, the close relation between E.R. and plastids.

In what concerns the release of the secreted product from the sub-cuticular space, it can occur by pores through the cuticle or by its rupture. In *Cistus* capitate trichomes the exudate is released by rupture of cuticle, as it happens in other oil secreting trichomes (Schnepf, 1972; Dell, McComb, 1977; Hammond, Mahlberg, 1977)

As we have referred in Results, the amount of resin secretion reach the maximum in later Spring and Summer. According Dell's hypothesis (1976) concerning the function of resins and glandular hairs in different western Australian plants, we can suppose that, in this period of the year, the great amount of resin in *Cistus monspeliensis* leaves must play a role in the reduction of cuticular transpiration or in the increase of reflectance of light from the leaf surface.

b) Bulbous trichomes

Secretory cells with wall ingrowths are re-

garded as transfer cells. Pate and Gunning (1972) have assumed that transfer cells are implicated in short distance transport.

The great enlargement of the plasmalemma surface area by the infoldings and the abundance of well organised mitochondria, suggest a high metabolic activity, probably associated with an active transport of solutes across the plasma membrane.

The abundant plasmodesmata observed in transverse walls, allow us to suppose that an intense flow of material via symplast may occur.

The close association between E.R. profiles and plasmalemma infoldings strongly suggest a functional role, presumably of E.R., in the transport of solutes to the plasmalemma or providing material for the plasmalemma or for the wall.

The labyrinthiform pattern of trichomes head cell walls seems to reveal an apoplastic transport of solutes within these walls.

The lateral cutinised stalk cell wall and its adhesion to the plasmalemma, may prevent release of metabolites to or from the epidermal cells via apoplast. Similar ultrastructural features have been observed and identically interpreted by authors in working with salt glands (Shimony, Fahn, 1968; Levning, Thomson, 1971; Perrin, 1971; Shimony *et al.*, 1973).

In the case of the bulbous trichomes organisation of the protoplast and of the walls seem to indicate that both pathways of water and ions are important and, probably, can occur.

In conclusion, the presence of Transfer cells in *Cistus monspeliensis* bulbous trichomes allows us to suppose that they play an important role in the absorption or secretion of water and salts in order to maintain a water balance within the plant.

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EXPLANATION OF PLATES

Abbreviations : CU cuticle; CW cell wall; D dictyosome; ER endoplasmic reticulum; M mitochondria; Nu nucleoli; Pl plastid; OR oleoresin; RER rough endoplasmic reticulum; V vacuole; Ve vesicle

Plate I

Fig. 1 and 2 - Scanning electron micrographs of *Cistus monspeliensis* trichomes. Fig. 1 Abaxial surface of the leaf with abundant non glandular trichomes and few bulbous trichomes (arrow). Fig. 2 Capitulate trichome (arrow) on the leaf adaxial surface.

Fig. 3 and 6 - Fluorescence micrographs of cross sections in the leaf. Fig. 3 Great amounts of oleoresin (OR) filling the spaces between the trichomes. Fig. 6 Capitulate trichomes showing autofluorescence in the upper cells of the glandular heads (arrow).

Fig. 4-5 and 7-8 - Semi-thin sections. Fig. 4 Mature capitulate trichome. The oleoresin is viewed in the cytoplasm and vacuoles. The cuticle is detached and broken. Subcuticular space is empty. Fig. 5 Cross section of a young leaf. Note the presence of a young capitulate trichome and two non glandular trichomes in early ontogenic stages. Large deposits of tannins are observed in some epidermal and parenchyma cells. Fig. 7 Mature capitulate trichome showing the sub-cuticular space (asterisk). Fig. 8 Capitulate trichomes surrounded by oleoresin.

Plate II

Fig. 1 - Portion of a capitulate trichome head cell showing the characteristic features of secretory cells - cytoplasm rich in ribosomes, plastids and mitochondria.

Fig. 2 - Detail of a young capitulate trichome glandular cell. A dictyosome with 5 flat cristae, and Golgi vesicles are seen.

Fig. 3 and 4 - Capitulate trichomes head cells in secretory phase. Fig. 3 An extensive network of E. R. is evident through the cytoplasm rich in ribosomes is observed. Mitochondria well structured and active and dictyosomes are abundant.

Fig. 5 - Glandular head cell of a young capitulate trichome. Parallel R E R profiles are near the plasmalemma.

Plate III

Fig. 1-4 - Glandular head cells of capitulate trichome during the secretory period. Fig. 1 - Mitochondria with well structured cristae are abundant. Plastids with few thylakoids and osmophilic droplets are observed. Fig. 2 - Swollen E R profile with electron dense material. Fig. 3 Coalescing vacuoles containing oleoresin-like material adherent to the tonoplast are seen. Fig. 4 - Large deposit of electron dense material in the sequence of vacuoles coalescence.

Plate IV

Fig. 1-3 Plastids in close association with ER

profiles.

Fig. 1 - Plastid surrounded by E R profile. Fig. 2-3 High magnification of plastids. Fig. 2 Portion of a plastid illustrating a close connection of periplastidial E R with plastid membranes (arrows).

Fig. 3 Detail of a plastid. Ribosomes can be seen only on the cytoplasmic face from E R profile (strong arrow).

Fig. 4-6 - Glandular upper cell of a capitulate trichome in secretory phase. Fig. 4 Cuticle is evident.

Fig. 6 The cuticle is detached from the microfibrillar layer of the wall. The sub-cuticular space (asterisk) is empty. Fig. 5 Longitudinal section of capitulate trichomes. Fig. 5a General view of a trichome in secretory phase. It is possible to see two stalk cells and a glandular head formed by six cells. Fig. 5b Magnification of the trichome upper cell. The empty sub-cuticular space is evident (asterisk). Fig. 5c Senescent trichome showing cellular desorganisation. The cuticle is broken (arrow).

Plate V

Fig. 1 - Bulbous trichome. The two head cells are typical transfer cells. The stalk cuticle is cutinised and adherent to the plasmalemma (strong arrow). Plasmodesmata (arrows) and mitochondria are abundant.

Fig. 2 - Glandular head cells. Dense cytoplasm rich in ribosomes and mitochondria. Large nucleus with clusters of chromatin and a great number of small vacuoles, containing probably salts, are observed. Plasmodesmata (arrows) are well seen.

Fig. 3 - Portion of a glandular cell wall showing a large cuticle and osmophilic droplets crossing the fibrillar layer of the wall. Fig. 4 - Detail of glandular cell wall. The labyrinthiform pattern of the wall is evident. Plasmodesmata (arrows) in cross section are well seen. Fig. 5 - Great number of mitochondria are aligned to the plasmalemma. Plasmodesmata are well observed (arrows).

Plate VI

Fig. 1 - Electron dense material crossing the microfibrillar layer of the wall. Wall ingrowths are followed by the plasmalemma. Small vacuoles, containing presumably salts, are numerous. Fig. 2 - Parallel R E R profiles are near the plasmalemma.

Fig. 3 - 4 and 6 - Different aspects of the close association between R E R and plasmalemma (strong arrow). Polysomes are well seen (arrow). Fig. 5 Mitochondria is located between two plasmalemma foldings.

Plate I

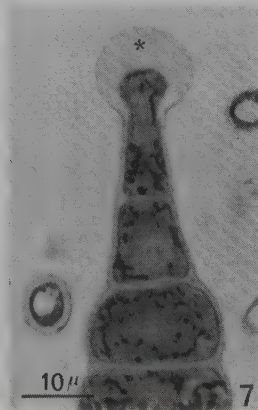
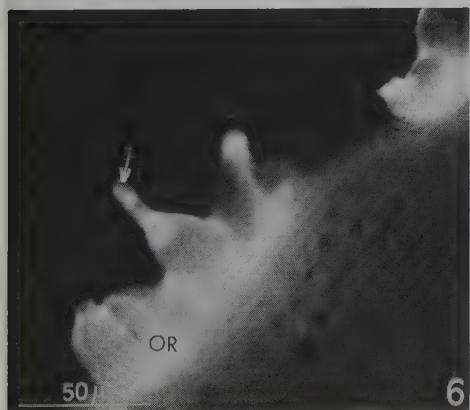
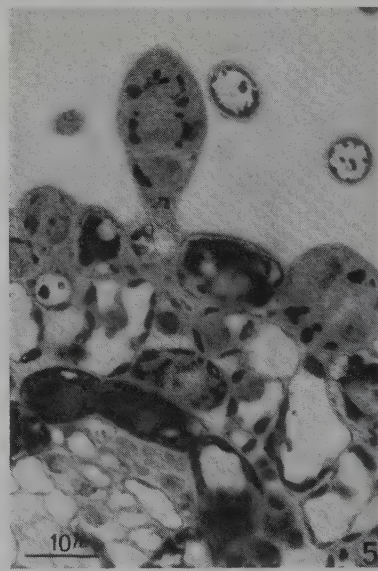
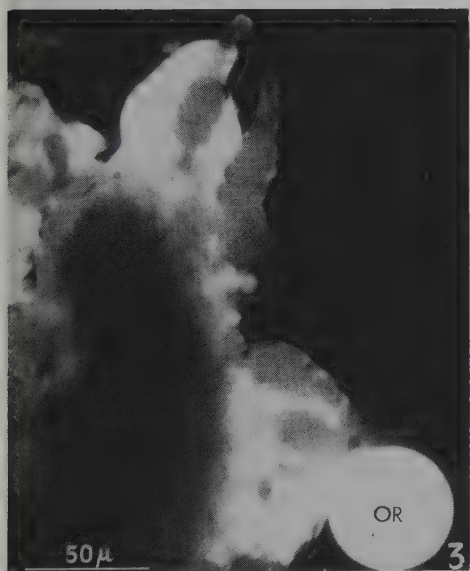
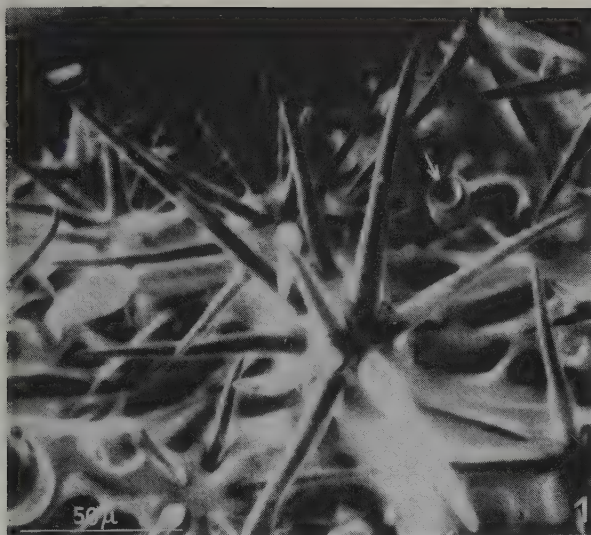


Plate II

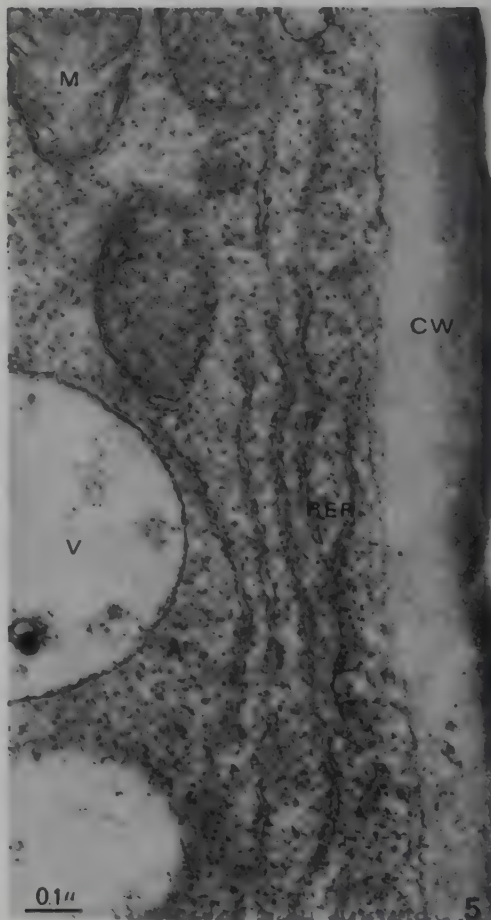
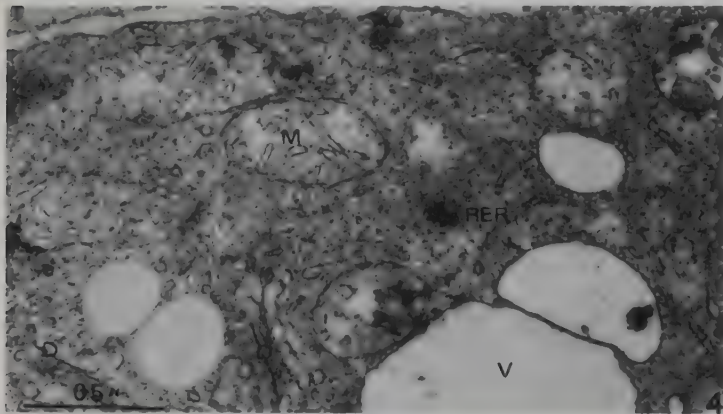
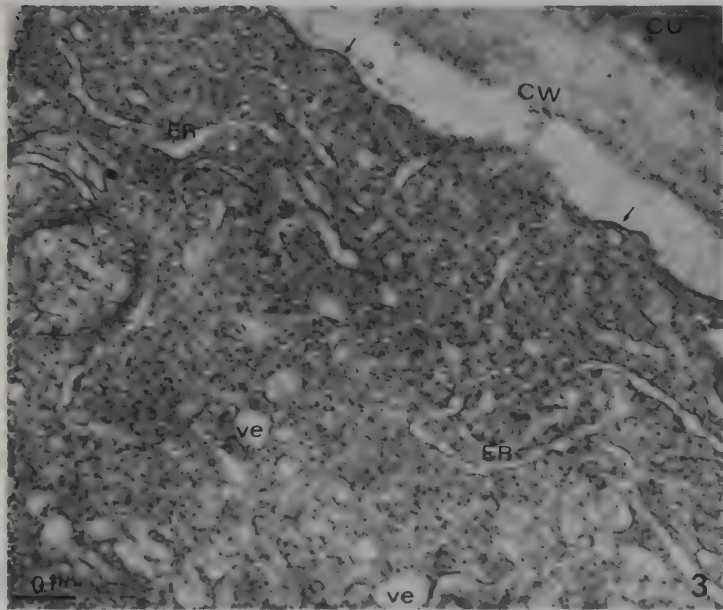
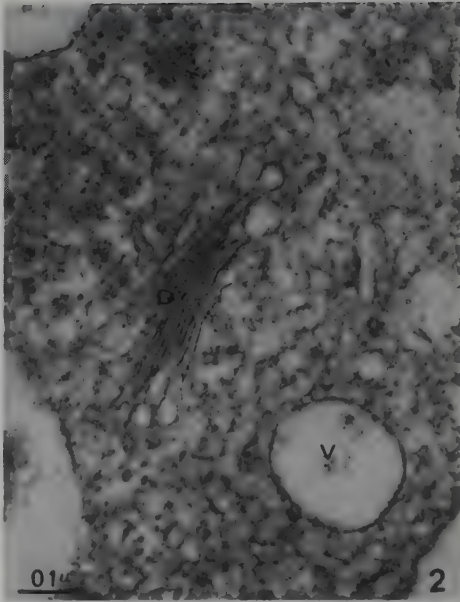
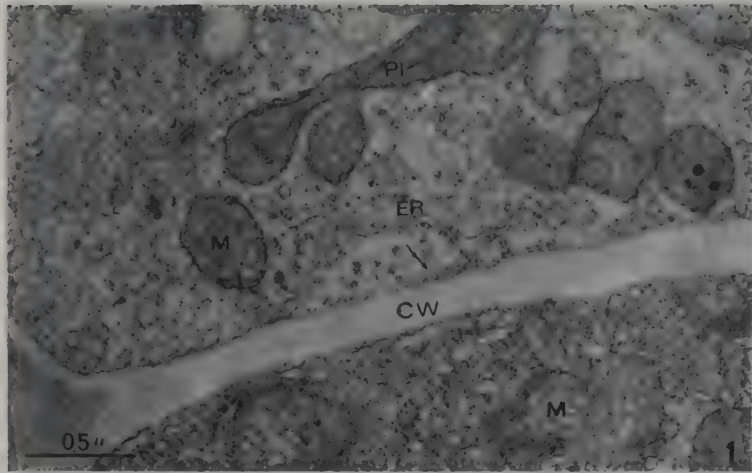


Plate III

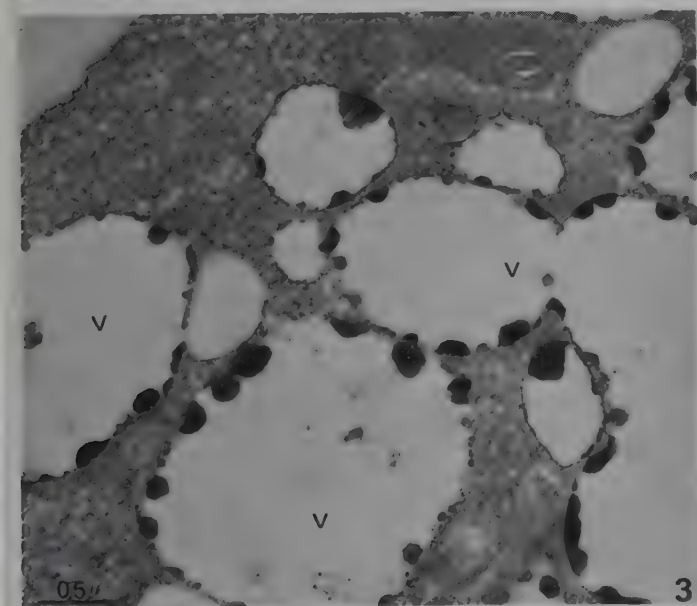
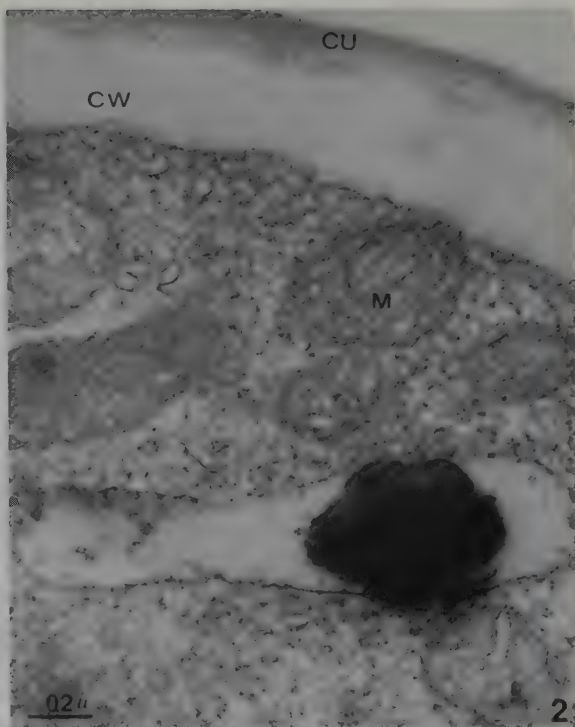
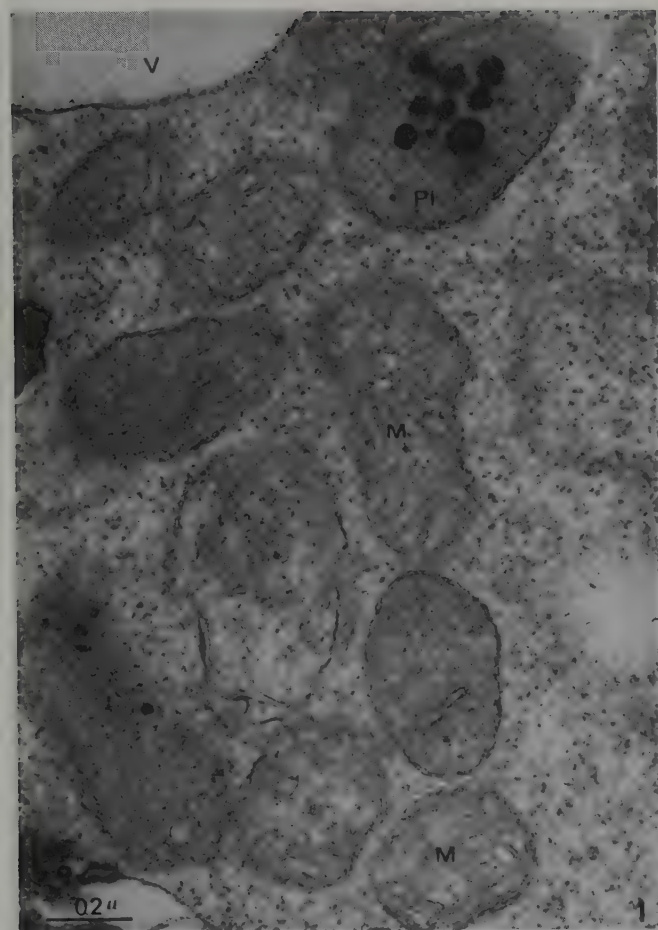
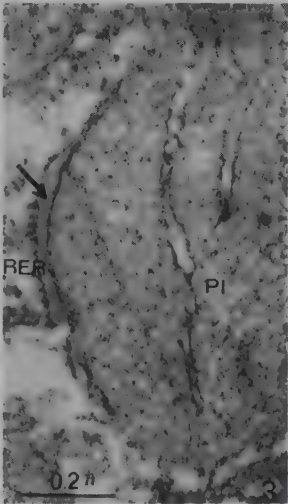
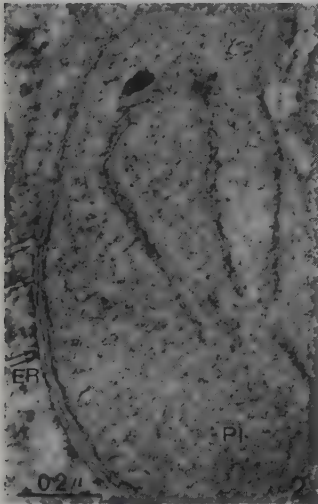
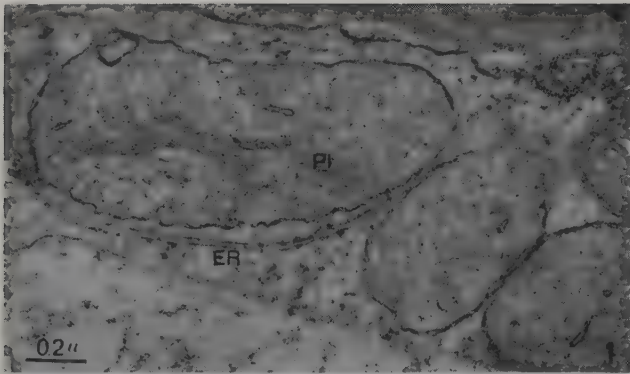


Plate IV



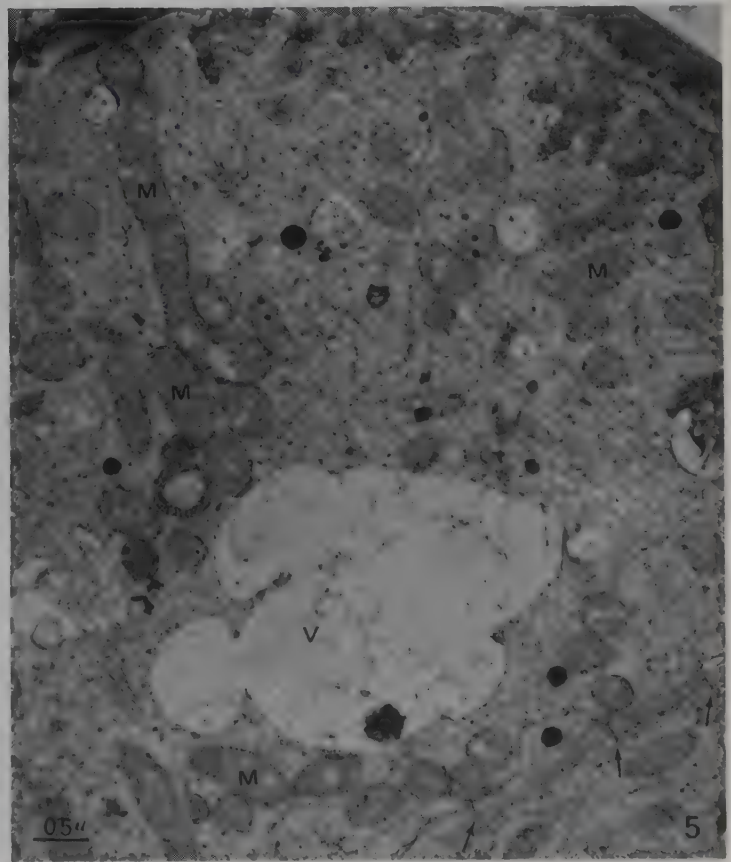
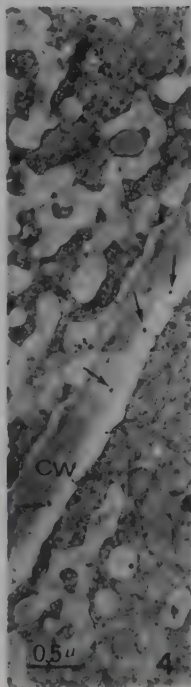
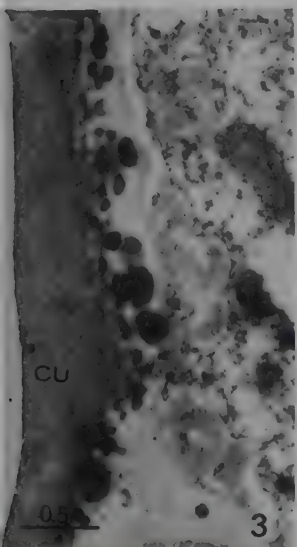
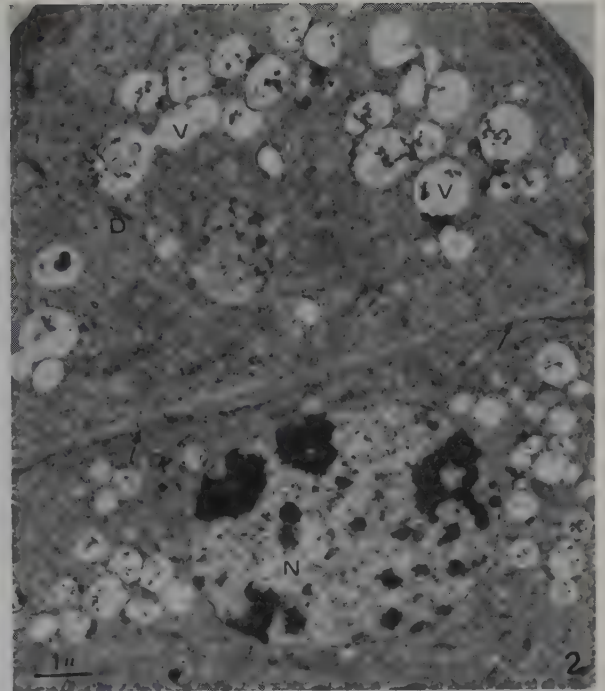
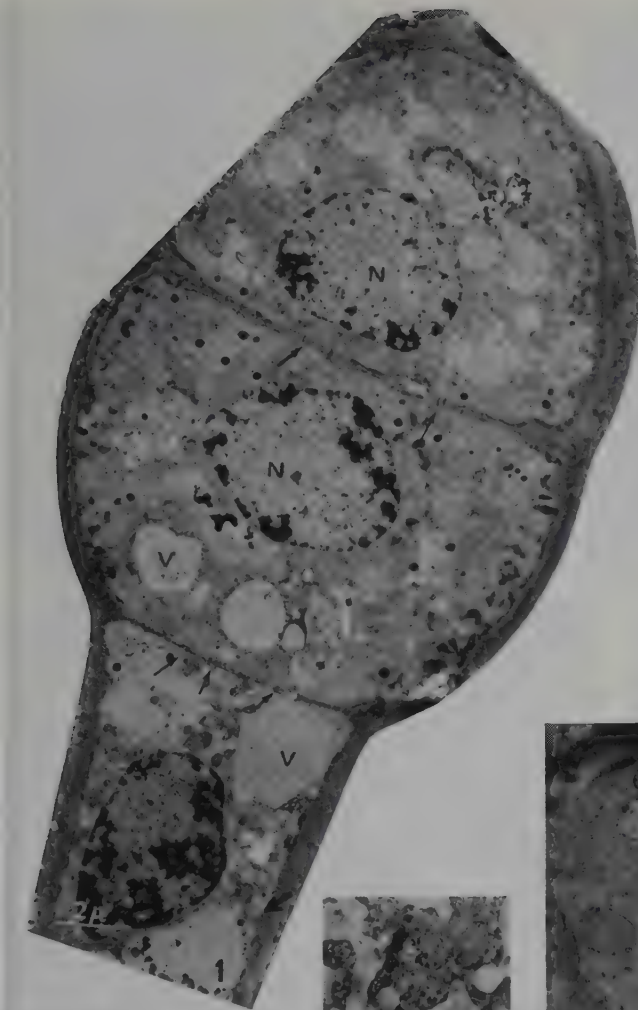
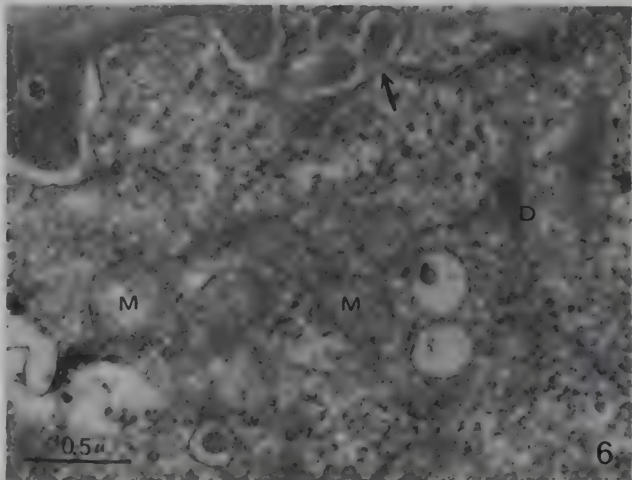
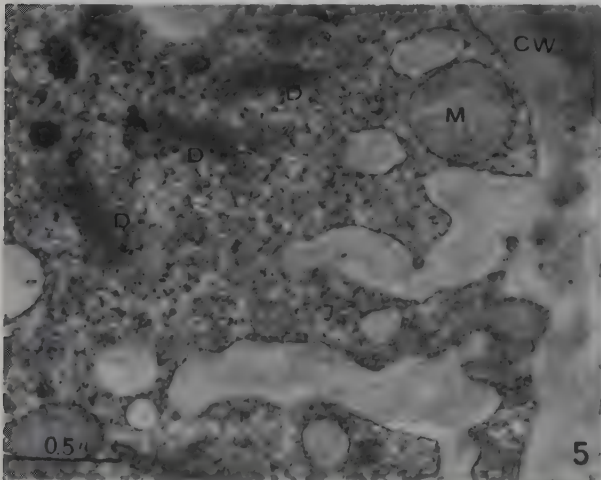
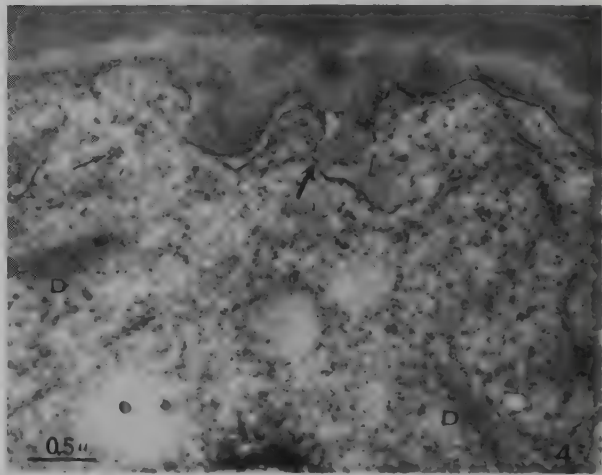
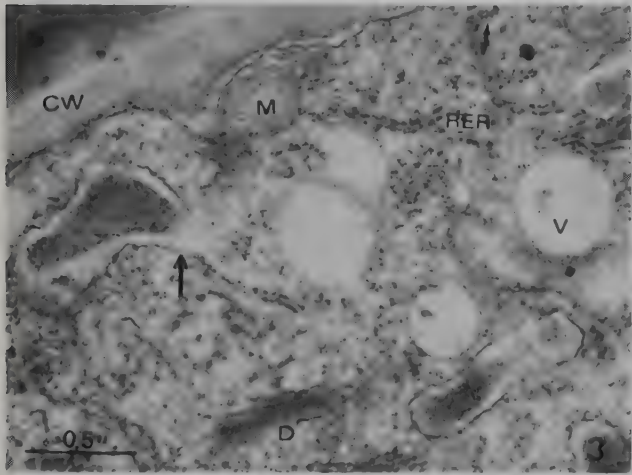
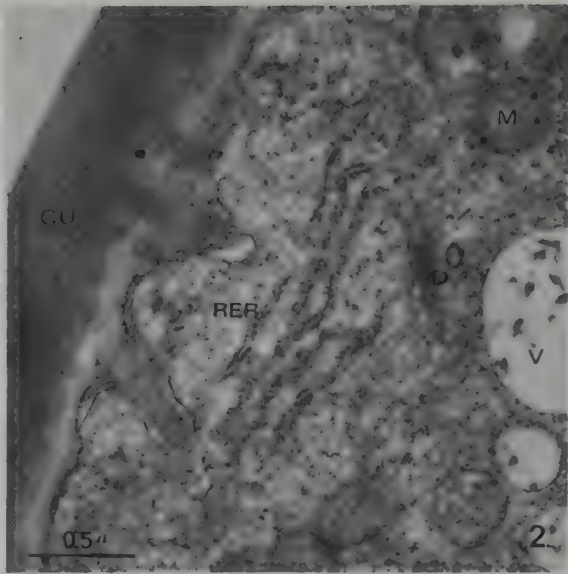
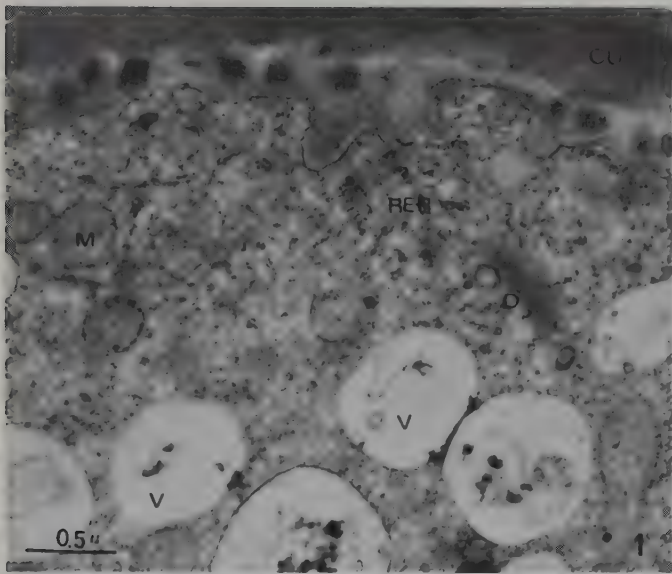


Plate VI



PART TWO

PHOTOSYNTHESIS AND ALLOCATION

The long summer drought that characterizes mediterranean-climatic regions places severe constraints on the photosynthetic potential of the resident plants. In this section a variety of mechanisms are described that characteristic evergreen plants inhabiting these regions have evolved to adapt to the drought. These include such physiological mechanisms as osmoregulation in the case of Olea to midday stomatal closure in the case of Arbutus. Allocation to root biomass is also an important adaptive mode for enhancing drought tolerance by certain species. Differential allocation patterns apparently explain dissimilar productivities of Mediterranean pines which have similar photosynthetic capacities. Although there appears to be a great variation in the photosynthetic response patterns of evergreen sclerophylls to drought, there is little difference in their light and temperature responses, at least of those species native to California and Chile. For example, they all are rather photosynthetically insensitive to temperature. It appears that, in contrast, some of the evergreen sclerophylls of the Mediterranean Basin have depressed photosynthetic rates at low temperatures. This difference needs to be studied further to determine its generality, and, if confirmed, could relate to the origins of the biota among the different mediterranean-climatic regions. Studies are also presented here that confirm the great differences in the photosynthetic potential of evergreen sclerophylls from that of drought-deciduous species. The significance of this difference has been related previously to the differential distributions of these types in relation to habitat aridity. It appears that those features of drought-deciduous species that result in their having a high photosynthetic capacity also result in their being more sensitive to atmospheric pollutants than evergreens. Our knowledge of the photosynthetic capacity of mediterranean-climate plants has progressed greatly in the past decade. As can be seen in the studies presented here, methods are now being utilized that permit precise measurements to be made on in situ native plants. The basis for the differences in responses between leaves on the same plant as well as those among plants is now being elucidated. We are approaching a comprehensive understanding of the variety of mechanisms with which mediterranean-climate plants enhance their productive capacity under conditions of severely limited resources, in particular water and nutrients.

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LEAF AGE EFFECTS ON THE CARBON GAIN OF INDIVIDUAL LEAVES IN RELATION TO MICROSITE

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1. INTRODUCTION

The relationship between leaf age and photosynthesis has been studied in many plants.

Aspects of the problem that have received particular attention include the levels of photosynthetic enzymes (Zima, Sestak, 1979; Patterson et al. 1980), the light response of photosynthesis (Richardson 1957; Ludlow, Wilson 1971), and the sensitivity of the aging process to several environmental variables. Leaf aging has been studied in relation to mineral nutrition (Egli et al. 1978), water stress (Ludlow 1975), light availability (Jurik et al. 1979; Yamaguchi, Friend 1979) and source-sink relationships within plants (Sweet, Wareing 1966; Patterson, Brun 1980). Though a few investigators have speculated on the ecological and physiological benefits a plant might gain from using old leaves for nutrient storage (Hopkinson 1966) or from shedding parts (Thomas, Stoddart 1980), no one has studied the possibility that the changes in photosynthetic characteristics observed after the age of maximum photosynthetic capacity yield benefits in carbon gain.

Beginning with Monsi and Saeki (1953), many studies have considered the attenuation of light by arrays of leaves. A dominant theme among investigations predicting the leaf angle (Duncan et al. 1967), leaf size (Parkhurst, Loucks 1972), or pattern of succession (Horn 1971) that maximizes carbon gain, is that optimal leaves at the top and bottom of the canopy should possess different morphological and physiological characteristics.

The growth form of most erect plants tends to position old leaves deeper in the canopy than young leaves, creating microsites in which old

leaves are frequently shaded. If natural selection has molded leaf aging in response to the probability of increasing shade with leaf age, the aging process may represent shade adaptation.

This study is the first in a series of analyses of leaf age and photosynthesis. It is aimed at testing the hypothesis that physiological leaf aging is not deterioration but adaptation in the sense that by increasing the long-term, net carbon dioxide fixation of individual leaves, aging increases a plant's potential for growth, competition, and reproduction. Because this treatment includes no consideration of constraints on the plant's nutrient and water-use economies, it can be termed a cost-free analysis. Subsequent papers will examine age-specific changes in photosynthesis relative to the costs of constructing, supporting, and maintaining leaves.

2. PROCEDURE

2.1. Methods and approach

All measurements are from field-grown individuals of a single species, Lepechinia calycina (Benth.) Epl., a facultatively drought-deciduous shrub common in disturbed areas of the California chaparral. This species was chosen because the drought-deciduous habit imposes convenient constraints on leaf longevity, and because leaves are produced over a relatively long period each year. By manipulating water and light availability, it is possible to dramatically alter leaf duration. Carbon dioxide and water vapor exchange were measured in the field at the Jasper Ridge Biological Preserve (San Mateo County, California) with a portable, steady-state gas exchange system (C. Field, J. A. Berry, H. A. Mooney, unpublished).

Lepechinia normally bears leaves from December through June. In dry sites it is completely

deciduous but in moister sites retains a few green leaves. When watered through the summer drought, *Lepechinia* develops and maintains leaf biomass comparable to that in the normal growing season. Plants watered through the summer develop elongated stems on which little self shading occurs.

Summer-grown leaves on watered plants were chosen for a series of experiments comparing sun and shade leaves. The absence of self shading minimized overlap between effects due to leaf age and shade. Relatively constant weather during California's clear, dry summer ensured that leaves of different age were not exposed to large differences in temperature, daylength, or illumination. Comparisons between sun-grown and shade-grown leaves were based on measurements from a single shrub, one half covered with greenhouse shading screen to reduce available illumination by approximately 80%.

Calculations of daily carbon gain in measured microsites were based on photosynthetic responses measured in early March, a period of rapid leaf production before the initiation of flowering. Natural growing season rather than summer-grown leaves were chosen for these calculations because plastic responses to growth conditions may be important components of the leaf aging process.

Daily courses of radiation were measured in the canopies of the shrubs used for the March photosynthetic studies. Four silicon cells, filtered to exclude ultraviolet radiation, were placed in the position and orientation of leaves of known ages. Light intensities and temperatures were measured at half-hour intervals over several days.

3. RESULTS AND DISCUSSION

3.1. Light penetration

Leaf area indices in drought deciduous California shrubs are usually less than 2.5 with a mean of approximately 1.3 (Mooney et al. 1977). Using a light-extinction coefficient generally appropriate for chaparral shrubs (Miller 1981), a leaf area index of 1.3 reduce available illumination by approximately 60%. Including effects due to leaf inclination, light availability for leaves at the bottom of the canopy of a typical drought-deciduous, mediterranean-climate shrub should be less than 25% of the radiation incident on a horizontal surface above the canopy.

In a *Lepechinia* canopy, radiation through the course of a March day is consistently lower at the microsite of a 100-day-old leaf than at the site of a 30-day-old leaf or just above the canopy (Fig. 1). During eight days of environmental scans in well-developed canopies from March through May, radiation levels were significantly different among leaves of different ages ($p < .025$ by Friedman's test (Sokal, Rohlf 1969)). Errors introduced by the infrared sensitivity of

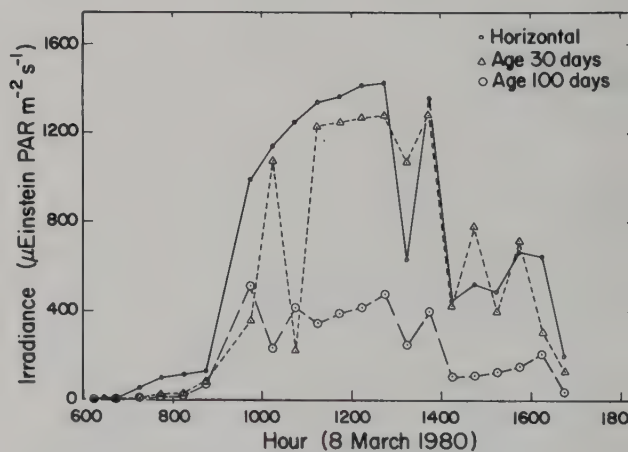


Figure 1. Photosynthetically active radiation for March 8, 1980 on a horizontal surface and in the microsites of leaves 30 and 100 days old.

the light sensors tended to underestimate the magnitude of the differences among leaves of different ages. Young leaves not quite fully expanded (20 to 40 d) were in the highest radiation environment. The two oldest pairs of leaves (80 to 100 d) were in the lowest. Microsites of 40 to 80-day-old leaves were intermediate in intensity. From over 100 scans during daylight hours, median intensities for the four age classes from youngest to oldest were 360, 340, 300 and 200 μ Einstein $m^{-2}sec^{-1}$.

3.2. Light adaptations

If aging processes adapt leaves to the lower illuminations they are likely to encounter in the autumn of their days, the photosynthetic responses of old leaves should be qualitatively

similar to those of younger, shade-acclimated leaves. Among shade-adaptable species or genotypes, growth under low illumination elicits several changes in leaf morphology and the light response of photosynthesis. These changes are general enough that it is possible, for comparative purposes, to identify a shade acclimation syndrome (Larcher 1975). The relationship between the light curves of sun- and shade-acclimated individuals is qualitatively the same as that between sun and shade species (Boardman 1977).

3.3. Effects of shading

Lepechinia responded to reduced illumination during growth with typical adjustments in photosynthetic characteristics (Table 1). In a comparison based on one leaf-age series of sun-grown leaves and one of shade-grown, light-saturated net

TABLE 1. A comparison of the sun-grown and shade-grown age series

		Ps max	Ps max	Resp	Resp	%N	N/area	Quantum yield	Spec. leaf weight	Light for sat.
		$\frac{\mu mol CO_2}{m^2 sec}$	$\frac{\mu mol CO_2}{g sec}$	$\frac{\mu mol CO_2}{m^2 sec}$	$\frac{\mu mol CO_2}{g sec}$		$\frac{g}{m^2}$	$\frac{\mu mol CO_2}{\mu mol hv}$	$\frac{g}{m^2}$	$\frac{\mu E}{m^2 sec}$
Effect of age*		p<.001	p<.05	p<.025	p<.025	p<.05	p<.05	n.s.	n.s.	n.s.
Effect of light*		p<.005	n.s.	n.s.	n.s.	n.s.	p<.005	n.s.	p<.01	p<.01
Mean, sun leaves		20.62	1.71	1.19	.0103	1.95	2.38	.0536	126.9	1410
Mean, shade leaves		12.98	.164	0.89	.0110	1.96	1.56	.0556	79.9	680
Environment	Age days									
sun	22	24.2	.246	2.15	.0218	2.67	2.62	.064	98.1	1600
	40	22.8	.173	1.60	.0130	2.13	2.81	.050	131.9	1500
	61	23.6	.212	0.70	.0064	2.23	2.48	.059	111.2	1700
	88	20.0	.139	0.90	.0064	1.70	2.43	.048	142.9	1600
	119	12.5	.084	0.60	.0041	1.03	1.55	.047	150.1	650
shade	18	13.2	.174	1.40	.0184	2.32	1.76	.062	75.9	700
	43	15.5	.164	1.45	.0152	1.95	1.85	.049	94.9	900
	55	16.9	.238	0.90	.0127	2.19	1.56	.059	71.2	800
	81	12.2	.150	0.35	.0043	1.76	1.43	.058	81.3	550
	122	7.1	.093	0.35	.0045	1.56	1.19	.050	76.3	450

*Significance evaluated by a two-way ANOVA without replication.

photosynthesis per unit area (P_a) decreased by 37% ($p < .005$). The light required to saturate photosynthesis decreased by 54% ($p < .01$). The dark respiration rate per unit area (R_a) appeared to decrease, but neither R_a nor the quantum yield (the efficiency of light utilization at low intensities) was significantly changed by shading. These results parallel those from many studies except that, in most cases, R_a did decrease with shading (Björkman, Holmgren 1963; Björkman et al. 1972; Singh et al. 1974).

Growth under reduced illumination often elicits decreases in specific leaf weight (Nobel et al. 1975; Wallace, Dunn 1980). Diplacus aurantiacus, another drought-deciduous shrub of the California chaparral, responded to shading with decreases in specific leaf weight proportionally greater than or equal to the decreases in P_a . Light-saturated net photosynthesis per unit weight (P_w) did not, in general, decrease in response to growth under reduced light. P_w was maximum for an intermediate growth illumination (Gulmon, Chu 1981). In response to shading, specific leaf weight in Lepechinia decreased by 37% ($p < .01$) (Table 1). P_w was not affected by 80% shade. The decrease in P_a with shading was caused entirely by the decrease in specific leaf weight. Dark respiration per unit weight (R_w) was also unaffected by shading.

Björkman and Holmgren (1963) and Gulmon and Chu (1981) report that shading decreased leaf contents of total organic nitrogen expressed on the basis of leaf area (N_a), but that growth under low illumination either increased or did not change nitrogen contents per unit leaf weight (N_w). Shading in Lepechinia decreased N_a ($p < .005$) but did not change N_w (Table 1).

3.4. Effects of age

In Lepechinia, the effect of leaf age on P_a was highly significant ($p < .001$) (Table 1). The oldest leaves from each growth condition had P_a 's approximately half those achieved by the most photosynthetically active leaf on the same stem. R_a decreased with age ($p < .025$) and the quantum yield was unchanged. The effect of leaf age on the light required to saturate photosynthesis was not significant when sun-grown and shade-grown series were considered together but was significant over two age series of sun-grown leaves ($r = -.83$, $p < .05$).

Specific leaf weight was not significantly affected by leaf age. The marked decreases in P_a and R_a with age were accompanied by similar decreases in P_w ($p < .05$) and R_w ($p < .025$). N_w and N_a both decreased significantly ($p < .05$) as leaves aged.

The qualitative correspondence between leaf aging in the absence of self shading and shade acclimation is excellent if the analysis is limited to area-specific or weight-independent physiological parameters. In Lepechinia, N_a , P_a , and the light required to saturate photosynthesis decreased with leaf age and with growth under shade. R_a decreased with leaf age and appeared to decrease with shading but the effect of shade was not significant. Neither leaf age nor shading affected the quantum yield of photosynthesis. In a weight-specific analysis, leaf aging and shade adaptation were quite different. N_w , P_w , and R_w all decreased with leaf age but were unchanged by shading. Age-specific changes in P_a and R_a were caused by changes in the activity or composition of a unit of leaf biomass. With shade acclimation, changes in area-based parameters were caused by changes in the amount of biomass per unit of leaf area.

In the context of identifying an adaptation, leaf aging should be compared with responses to growth under reduced illumination on the basis of those parameters which increase the carbon gain of

shade-grown leaves relative to sun-grown leaves, in low-light environments. Comparisons based on net photosynthesis per unit leaf weight allow the assessment of carbon gain as a return on an investment in leaf biomass. With shade acclimation in *Lepechinia*, increased low-light photosynthesis per unit weight resulted primarily from decreases in specific leaf weight. Leaf aging in *Lepechinia* did not decrease specific leaf weight but did decrease R_a , thus increasing net photosynthesis at low illumination on weight and area bases.

Light curves from a summer-grown, full-sun leaf-age series in *Lepechinia* reveal that, at very low light intensities, net photosynthesis increased with increasing leaf age (Fig. 2). At a light intensity as low as $100 \mu\text{Einstein m}^{-2}\text{sec}^{-1}$, net photosynthesis was largely independent of leaf age (Fig. 3). The upper limit to the range of light intensities over which reduced R_a endowed increased net photosynthesis was set by the beginnings of early light saturation in the older leaves.

3.5. Leaf nitrogen, respiration, and photosynthesis

Since, with leaf age, decreases in dark respiration were responsible for increased net photosynthesis at low-light intensities, it is relevant to consider the factors controlling dark respiration and the ramification of that control.

Before the age at which leaves reach full expansion, respiration has components due to growth and maintenance (McCree 1970). As leaf expansion slows and stops, the growth or construction component disappears. At the age of full expansion, dark respiration in *Lepechinia* had declined to as little as one half the rates measured in the youngest leaves. After full expansion, respiration continued to

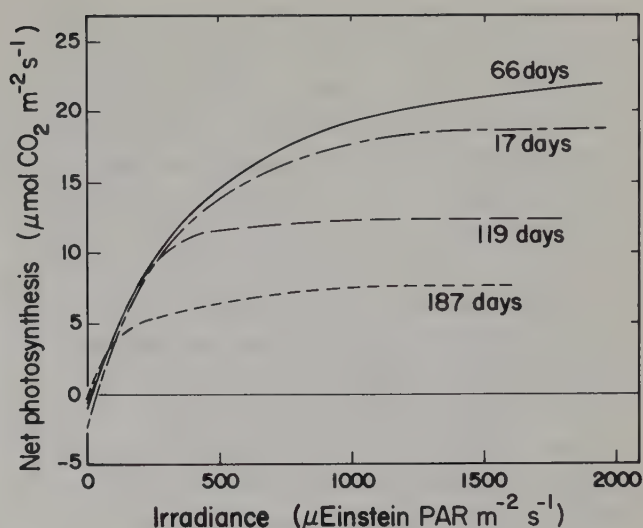


FIGURE 2. Light response curves for an age series of summer-grown leaves from an unshaded plant. Numbers refer to leaf ages in days.

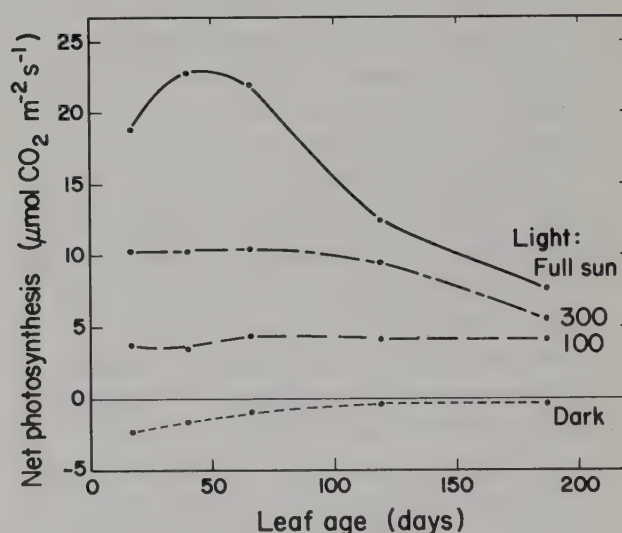


FIGURE 3. Net photosynthesis per unit area as a function of leaf age at several light intensities. Light intensities are in $\mu\text{Einstein m}^{-2}\text{sec}^{-1}$. Data are from the leaf age series described in Figure 2.

decrease, falling approximately threefold by the onset of yellowing prior to abscission (Table 1). Similar results were obtained by Richardson (1957) and Jurik et al. (1979). Woolhouse (1967) and Syvertsen and Cunningham (1977) found no decrease in dark respiration with leaf age.

The major energy consumption process in maintenance respiration is protein turnover (Penning de Vries 1975). Decreases in crude plant protein per unit weight, values quantitatively related to N_w (Wall et al. 1974), should decrease protein turnover and R_w . For 40 *Lepechinia*, leaves of many ages and from several growth conditions, R_w was highly correlated with N_w ($r = .640$, $p < .001$). After the age of full expansion, nitrogen export may be responsible for leaf-age-dependent decreases in dark respiration.

Variations in N_w had important consequences for photosynthetic performance at high light availability. P_w was highly correlated with N_w ($r = .926$, $p < .001$) for sun and shade-grown leaves (Fig. 4). A correlation between nitrogen and photosynthesis has been observed in *Eucalyptus* species native to different habitats (Money et al. 1978), in *Diplacus aurantiacus* grown under several nitrogen and light regimes (Gulmon, Chu 1981), and in wheat leaves of different ages grown at several nitrogen availabilities (Osman, Milthorpe 1971). The correlation is not unexpected in light of the correlation between ribulose-1,5-bisphosphate carboxylase activity and maximum photosynthesis (Medina 1971; Björkman 1979; Wong 1979) and the contribution of this enzyme to total leaf protein (Björkman 1973).

Since leaf nitrogen content of some factor highly correlated with it appears to limit both respiration and photosynthesis in *Lepechinia*,

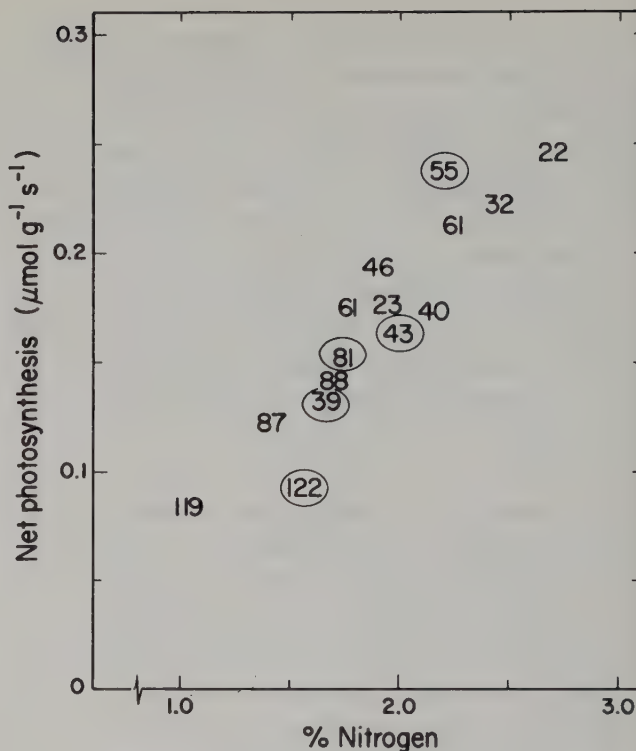


FIGURE 4. The relationship between maximum net photosynthesis per unit weight and leaf nitrogen content per unit weight. Values are from summer-grown leaves. Numbers refer to leaf ages in days. Circled numbers are the ages of shade-grown leaves. ($r = .926$ $p < .001$.)

the maximization of carbon gain involves a trade-off. High nitrogen contents maximize carbon gain for leaves exposed to high illumination, but low nitrogen contents yield maximum carbon gain for leaves exposed to low-light availability.

3.6. Carbon gain in measured microsites

Aging is adaptive in the carbon-gain sense if old leaves tend to occupy microsites where they realize more long-term net CO_2 fixation than would leaves that had not aged. To test the adaptation hypothesis in *Lepechinia*, the observed aging pattern was compared with a conceptual alternative model without physiological aging beyond maturity. In the alternative model, leaves were assumed to

maintain maximum photosynthetic capacity from the normal age of peak photosynthetic activity through the rest of their life spans. Carbon gain for the observed and hypothetical patterns was calculated on the basis of leaf weight.

To calculate daily carbon gain for each leaf in the age series at every microsite, photosynthetic rates were calculated from the light intensities measured every half hour and the light response curves of each leaf. Photosynthesis per half hour was summed over each day. Through the dark period, respiration rates were calculated for every half hour from the measured respiration rates, measured temperatures, and an assumed Q_{10} of two for dark respiration. Total night respiration was then subtracted from integrated daily photosynthesis to yield daily net carbon gain for each leaf in each microsite. The calculations did not include corrections for the temperature or vapor pressure deficit responses of photosynthesis. *Lepechinia* had a broad temperature optimum for photosynthesis with rates over 90% of the maximum from 14° to 35°. This is similar to the broad optima observed in other chaparral species (Mooney et al. 1975; Oechel et al. 1980) and suggests that temperature does not alter the relative performance of leaves of different ages. Vapor pressure deficits during the days considered were great enough to cause significant reductions in stomatal conductance but could have imposed only slight reductions in photosynthesis (unpublished data).

To calculate total carbon gain for the observed aging pattern, daily net carbon gain was summed over the leaf-age series. The value chosen for each leaf was the one expected in the microsite appropriate for the leaf's age. For the model without physiological aging, carbon gain was summed over the same array of microsites, but the values chosen for leaves older than 36 days

were from the 36-day-old leaf, the leaf with the maximum photosynthetic capacity. Values for leaves younger than 36 days were not altered. The comparison between the observed pattern and the no-aging model is shown in Table 2. For March 7-8, performance from the two aging patterns was almost identical. The observed pattern yielded more carbon gain for April 4-5 and less for April 17-18. The proportional difference between the no-aging and the observed strategies depended on mean integrated daily radiation over the measured microsites (Fig. 5). At mean daily intracanopy radiation loads under $15 \text{ Einstein m}^{-2}\text{day}^{-1}$, the observed pattern gained more carbon than a no-aging strategy. In brighter environments, the no-aging strategy yielded higher returns. Intracanopy radiation is controlled by light intensity above the canopy and by canopy development. On dim days, or in canopies with high leaf area indices, the observed aging pattern yielded high returns. On Jasper Ridge, mean daily light intensities averaged over entire months in 1979 and 1980 are shown in Table 3. The January and February averages are below the horizontal radiation on March 7 and 8. Days in which the observed leaf-aging pattern gains more carbon

TABLE 2. Daily carbon gain ($\text{mmol CO}_2 \text{ g}^{-1}\text{day}^{-1}$) expected from the observed aging pattern and the alternative without physiological aging for 3 days in the spring of 1980. Irradiance is in $\text{Einstein PAR m}^{-2}\text{day}^{-1}$. Irradiance within canopy is averaged over four sensors.

	March 7-8	April 4-5	April 17-18
Irradiance within canopy	14.15	5.96	16.84
Carbon gain			
Observed pattern	17.53	11.00	27.37
Hypothetical strategy	17.59	10.10	28.54
Irradiance above canopy	23.31	14.99	47.73

TABLE 3. Mean irradiance (Einstein PAR $\text{m}^{-2}\text{day}^{-1}$) on a horizontal surface. Values are averages from continuous recordings in 1979 and 1980.

	January*	February	March	April
Irradiance	13.6	20.5	32.1	42.5

*Data from 1980 only.

than an alternative without physiological aging must occur with high frequency.

These carbon gain advantages, realized as a result of aging, depend only on the photosynthetic characteristics of individual leaves. As leaves age, they not only become shade adapted, but they also export nitrogen which becomes available for incorporation in other parts of the plant. Carbon gain increases from individual leaves combine with the effects of age-specific nutrient export and changes in water use to constitute the overall adaptive significance of leaf aging.

4. SUMMARY

Light availability decreased as leaves aged in *Lepechinia calycina*. Even when the growth form was modified to prevent self shading, qualitative aspects of the light response of photosynthesis were very similar between old leaves and younger leaves grown under artificially reduced illumination. Leaf aging without self shading and shade acclimation both tended to increase net photosynthesis per unit weight at low-light intensities. With shade acclimation, increased photosynthesis at low light was due primarily to decreased specific leaf weight. With aging, it was due to reduced respiration. Leaf nitrogen content appeared to control respiration and maximum photosynthesis in parallel. With aging, nitrogen contents consistent with high photosynthesis at

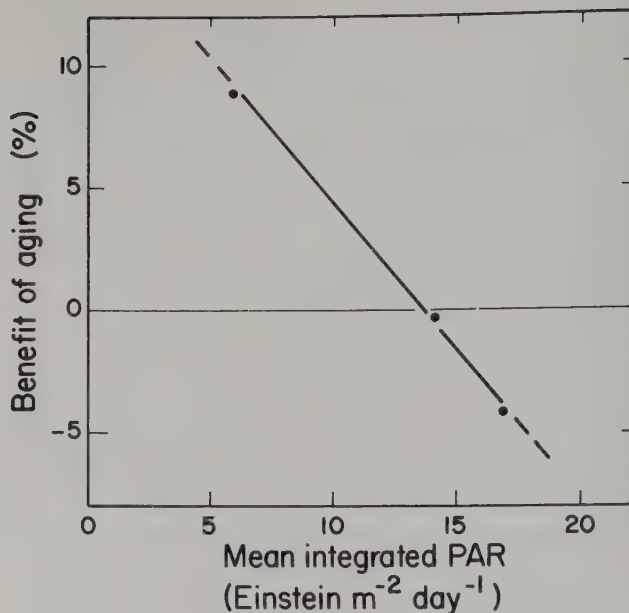


FIGURE 5. Proportional difference in daily carbon gain between the observed aging pattern and the hypothetical alternative without physiological aging as a function of the mean daily radiation in four leaf microsites. When the benefit is positive, the observed aging pattern realizes greater carbon gain.

low-light intensities were inconsistent with high photosynthesis at light saturation.

The daily carbon gain of a leaf age series was calculated from age-specific photosynthetic responses and light scans within a canopy. Daily carbon gain could be increased in simulations by replacing the actual leaf-age series with a hypothetical non-aging series, but only at high light. In the winter growing season, days in which the actual pattern outperforms the non-aging model must occur high frequency.

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NUTRIENT AND ENVIRONMENTAL CONTROLS ON CARBON FLUX IN MEDITERRANEAN SHRUBS FROM CALIFORNIA

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1. INTRODUCTION

Major limitations on carbon flux in chaparral vegetation are water, photoperiod, and temperature (Mooney et al., 1975; Oechel et al., 1980).

Nutrient availability has also been suggested as a major limitation of growth in chaparral (Christensen, Muller, 1975; Mooney, Gulmon, 1978) and may limit photosynthesis as well. The addition of fertilizer or ash to mature chaparral soils has been found to result in enhanced growth rates of chaparral species (Christensen, Muller, 1975).

While a net loss of many soil nutrients, including nitrogen, phosphorus, and potassium, can result from fire (DeBano, Conrad, 1978), nitrate, ammonia, phosphate, sulphate, and potassium availabilities may increase after the fire (Christensen, Muller, 1975). Assuming a 20% soil moisture content, calculations were performed on data of Christensen and Muller (1975) from a Zaca Lake, California burn over soils of Monterey shale parent rock. These calculations indicate that nitrogen availability at 0-2 cm increased from the equivalent of 12 mM nitrogen in unburned areas to 38 at the burn site. At 4-6 cm, available nitrogen was 8 and 17 mM nitrogen in the unburned and burned sites, respectively. Both nitrogen and phosphorus have been shown to limit chaparral growth rates in unburned soil. However, burning over chaparral soils nearly eliminates nutrient limitation of growth of two postburn species, *Centaurea melitensis* L. Tocalote and *Phacelia grandiflora* (Benth.) Gray. [*Eutocq. g.* Benth] (Christensen, Muller, 1975). Following fire, resprouts show enhanced photosynthetic rates. Resprouts from hand-cleared areas, however, may not exhibit elevated photosynthetic rates; Oechel and Hastings (1980) concluded that nutrient enhancement following fire might account for an increase in

photosynthesis of almost 500% in *Adenostoma fasciculatum* H. & A. burn resprouts.

While nitrogen has received most attention as a limiting nutrient in chaparral, several nutrients are potentially limiting. The nutrient(s) causing enhanced photosynthesis in resprouts following fire is(are) not known. Predictions are difficult since the nutrient controls of photosynthesis in wildland plants are poorly understood. However, nitrogen appears to be a prime limiting nutrient in the chaparral and is a logical starting point to elucidate nutrient controls on net carbon uptake. This paper reviews the limitations on photosynthesis by temperature and light and explores the extent to which nitrogen may be limiting photosynthesis and growth in the evergreen chaparral species *Ceanothus crassifolius* Torr. studied in the lab.

2. METHODS

2.1. Field gas exchange

Light and temperature dependency of photosynthesis were measured on field plants at 1000 m elevation at Echo Valley, California (32°54' N, 116°39' W). A six-cuvette infrared gas analysis system was used in conjunction with a computer controlled data acquisition system. Water vapor fluxes were measured using Vaisala thin film variable capacitance type humidity sensors. Plant samples were generally measured at temperatures between 5° and 40°C at 5° intervals. Samples were held at most temperatures for 24 h and measured during the natural excursion of solar radiation. These data allow a matrix of responses to various light and temperature combinations to be constructed (Oechel, Lawrence, 1979). The data were fit by nonlinear regression using a Michaelis-Menton form for the photosynthetic response to light intensity. The resultant regression was used to plot isopleths of equal photosynthetic rates in relation to combinations of temperature and light.

To perform the regression, photosynthetic rates for each species were grouped into one of 8, 5°C temperature intervals between 2.5 and 42.5°C with light intensities ranging from 0-2400 $\mu\text{E m}^{-2} \text{s}^{-1}$. For each temperature interval, CO_2 exchange was fitted to a Michaelis-Menton function of light. To transform the CO_2 flux data into a form suitable for the Michaelis-Menton regression a term equal to the value of dark respiration was temporarily subtracted from the CO_2 exchange rate during the curve fitting so that the expected value of the new CO_2 exchange rate equals zero at zero light. In addition, since the CO_2 response decreases at midday under water stress, only data from midnight to noon and light intensities no greater than 1800 $\mu\text{E m}^{-2} \text{s}^{-1}$ were used in the regression.

The nonlinear regressions were computed using the BIOMED statistical analysis program. Maximum photosynthetic rate (V_m) and half saturation constants (k) were obtained for each temperature interval and were matched with the mean observed temperature in that interval. From this matching both V_m and k were regressed on temperature and temperature squared (T , T^2). The exception to this was *Ceanothus greggii* Gray which, due to variability in k values, had k regressed on T^2 and T^3 (temperature cubed). Dark leaf respiration rates were regressed on T^2 for all species. This function was used for the dark respiration term which was subtracted from the rate of CO_2 exchange.

Combining the results of the above regressions, the following equation was obtained:

$$\text{PS} = [V(t)L]/[L + k(t)]$$

where PS is the photosynthetic rate ($\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) reduced by an amount equal to dark respiration [DRSP(t)]; $V(t)$ ($\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) is the predicted CO_2 uptake at nonlimiting light levels; $k(t)$ ($\mu\text{E m}^{-2} \text{s}^{-1}$) is the light level at one-half maximal CO_2 uptake, and is a function of temperature; DRSP(t) ($\Delta\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) is the CO_2 exchange at zero light, a negative number and a

function of temperature; and L is the light level ($\mu\text{E m}^{-2} \text{s}^{-1}$). Isopleths of equal photosynthetic rate were plotted with respect to temperature and light. A photosynthetic level was chosen and then light isolated as a function of temperature as follows:

$$L = \{k(t)[\text{PS} - \text{DRSP}(t)]\}/[V_m(t) - \text{PS} + \text{DRSP}(t)].$$

2.2. Response of CO_2 flux and growth to nitrogen treatment levels

Net photosynthesis and/or respiration of leaves and stems, and root respiration of *C. crassifolius* were examined under several regimes of light and temperature. Cuttings were taken from the San Dimas Experimental Forest Research site, rooted, and then transplanted in February 1979 into 10-liter plastic containers filled with 9 liters of washed #16 silica sand. The sand was washed by rinsing it three times with tap water followed by three rinses with deionized water. The containers were placed above tanks containing one-quarter strength Hoagland's solution adjusted to the specific nutrient treatment. Nutrient treatment consisted of 1.0, 2.5, 5.0, 10.0, and 15.0 mM nitrate levels with 0.5 mM phosphorus. In mid-June 1979, the nutrient treatments were changed to 1.0, 5.0, 10.0, 15.0, and 20.0 mM nitrate with 0.7 mM phosphorus. The nutrient solution was drawn from the tanks below. A drain in each container allowed excess liquid to return from the pot to the tank reservoir. Appropriate flow rates were determined, and for the first month the plants were watered for 15-min periods 5 times each day and once at night. During the second month they were watered three times a day.

From the third month until being transferred to San Diego State University in November 1979, the plants were watered for 20 min twice each day. At San Diego the plants were maintained in a greenhouse and irrigated with deionized water three to four times per week as needed until the conclusion of the experiment in January 1980.

Gas exchange measurements were made using a laboratory version of the field photosynthesis cuvette and data acquisition system described by Oechel and

Lawrence (1979).

Root respiration chambers were fashioned from small styrofoam ice chests which were cut in half, reduced in size, and then rejoined with silicone sealer. The plant pots (25-cm diameter) were sealed with clear acrylic plastic covers. A 55-cm hole in the center of the cover accommodated the plant stem. A number 11 rubber stopper was drilled so as to fit snugly around the plant stem, and then inserted into the hole in the cover. Smaller ports also sealed with stoppers were added to allow the insertion of thermocouples to measure soil temperature and for the insertion of air supply and return lines. Putty was used as a sealer when necessary. Copper coils were fashioned to surround the pots, and both pots and coils were then placed in the styrofoam ice chests. Root temperatures were controlled by circulating ethylene glycol solution through the coils with a Lauda K-2/R regulated bath. When measuring root respiration the air supply and return lines were removed from the photosynthesis cuvettes and appropriately attached to the root chamber gas exchange ports.

Gas exchange was initially examined in all plants at 25°C. Irradiance was adjusted to $1500 \mu\text{E m}^{-2} \text{s}^{-1}$ and steady state photosynthesis measured. This procedure was repeated for plants in complete darkness. Next the leaves were removed and the stem gas exchange measured under the same conditions. New branches were inserted in the chambers and the photosynthetic response to various regimes of light and temperature examined in replicates from the 1, 5, 10, and 20 mM nitrate treatments. Temperatures ranged from 5° to 35°C in 5° increments. Light levels were 0, 25, 50, 75, 150, 300, 600, 1200, and $1500 \mu\text{E m}^{-2} \text{s}^{-1}$.

Root respiration was measured over the same temperature range, with the shoot illuminated ($1500 \mu\text{E m}^{-2} \text{s}^{-1}$) or in the dark following a dark adaptation period of 24 h.

3. RESULTS AND DISCUSSION

3.1 Field gas exchange

Photosynthesis in *C. greggii* shows a broad and relatively temperature insensitive response pattern (Fig. 1). The maximum rate of photosynthesis is about $14 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ with a temperature optimum of about 20°C at light intensities above $1800 \mu\text{E m}^{-2} \text{s}^{-1}$. At the lower light intensities the temperature response is very flat and the position of the temperature optimum is, therefore, less important. At 5°C temperature and a light intensity of $1800 \mu\text{E m}^{-2} \text{s}^{-1}$, photosynthesis is above $10 \text{ mg dm}^{-2} \text{s}^{-1}$ or over 70% of the rate at optimum temperature.

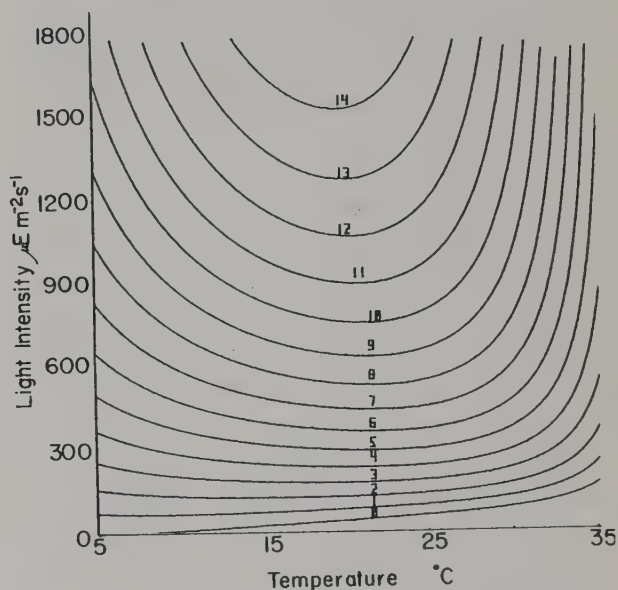


FIGURE 1. Isopleths of photosynthetic rates with respect to temperature and light intensity for *Ceanothus greggii* growing at Echo Valley, California in May 1976. Rates predicted with nonlinear regression analysis using a Michaelis-Menton form for the light response.

The regression used to produce the isopleths appears to be underestimating photosynthetic rate at higher temperatures and light intensities. The isopleths show photosynthetic rate at 35°C and $1800 \mu\text{E m}^{-2} \text{s}^{-1}$ to be about $5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ or 36% of the maximum photosynthetic rate at optimum temperature. Light saturation of the whole branch does not occur until light intensities of $1500 \mu\text{E m}^{-2} \text{s}^{-1}$ and greater

are reached at optimal temperatures. The Michaelis-Menton form appears to give a good fit to the data except at higher temperatures. And inspection of the data used in this regression indicates that the actual photosynthetic rate at 40°C is about 50% of the maximum photosynthetic rate (Oechel et al., 1980).

The results presented here for *C. greggii* are representative of other chaparral and matorral shrub species examined (Oechel et al., 1980). These other species also tend to have similar photosynthetic temperature optima and relatively high photosynthetic rates at 5° and 40°C.

3.2. Response of CO_2 flux and growth to nitrogen treatment levels

There was little increase in leaf nitrogen found with increasing treatment concentration. The average leaf nitrogen level at 1 mM nitrate was 15 ± 1 mg g dry wt⁻¹. A 20-fold increase in available nitrate resulted in only a 25% increase in leaf nitrogen. Little change in leaf phosphorus concentration among nutrient treatments was observed.

Leaf phosphorus concentration increased about 10% between 1 and 20 mM nitrate. Potassium concentration, however, increased markedly with increasing nitrogen concentration. At a 1 mM nitrate treatment potassium concentration was 4.9 ± 0.6 mg g dry wt⁻¹, while at a 20 mM nitrate treatment potassium leaf concentration had more than doubled to 11.1 ± 1.1 mg g dry wt⁻¹.

Despite rather large variability within treatments, increases in total aboveground growth were noted with nutrient treatment levels above 10 mM nitrate. The lowest growth rates occurred between 1 and 10 mM nitrate (Fig. 2). At 5–10 mM nitrate treatments, aboveground production was about 25 g dry wt over the period of the study. At 15 mM nitrate production was almost twice as high, 47 g dry wt, and at 20 mM nitrate growth was 107 g dry wt. Thus, the growth rate at 20 mM nitrate was over 4 times that at the 5–10 mM nitrate treatment levels.

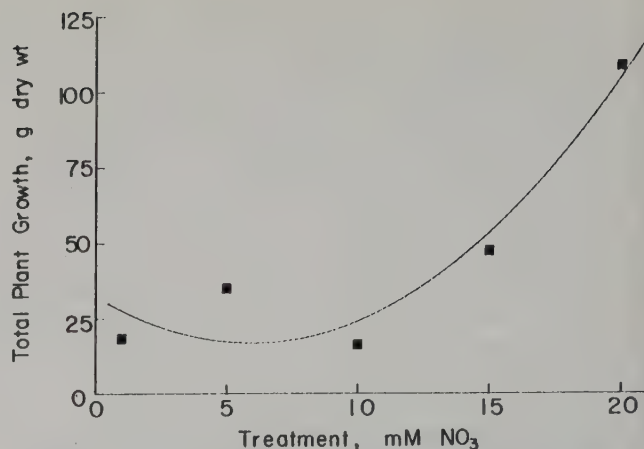


FIGURE 2. The response of total aboveground biomass production to varying nitrogen treatment levels ($r = 0.82$, $R^2 = 0.91$).

Surprisingly, the response of net photosynthesis was quite different from that of growth. The highest photosynthetic rates were found at treatment levels of from 1 to 10 mM nitrate. At these treatment levels, photosynthesis was between 31 and 35 mg CO_2 dm⁻² h⁻¹. Net photosynthetic rate fell to 22 mg CO_2 dm⁻² h⁻¹ at nutrient treatment levels of 15 mM nitrate and to 18 mg CO_2 dm⁻² h⁻¹ at 20 mM nitrate (Fig. 3). This represents almost a 50% reduction in photosynthesis from the rate at the 1 mM nitrate treatment to that which occurs when the plant is grown at 20 mM nitrate. Leaf respiration also showed a fairly consistent decline in rate between the 1 and 20 mM nitrate treatments. Respiration rate declined from 9 mg CO_2 dm⁻² h⁻¹ at 1 mM nitrate to 4.5 mg CO_2 dm⁻² h⁻¹ at 20 mM nitrate (Fig. 3). This consistent decrease in respiratory rate may indicate lower enzyme concentrations and/or lower protein turnover rates at the higher treatment levels.

Virtually any essential nutrient can occur in sufficiently limiting quantities to inhibit photosynthesis. The results reported here may be due to a dilution of essential nutrients other than nitrogen which causes a suppression of photosynthesis. A survey of leaf tissue nutrients indicated little correspondence between most essential nutrients and photosynthetic rates under the observed treatments.

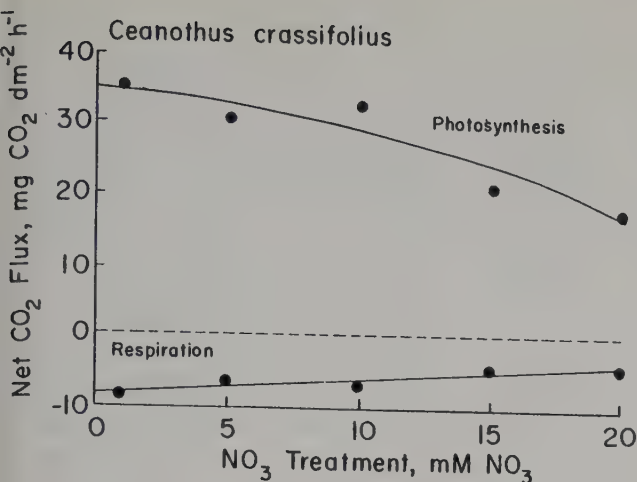


FIGURE 3. The relationship between nitrate growth treatments and photosynthetic and respiratory rates (r) in *Ceanothus crassifolius* ($r = -0.93$ and 0.94 , $R^2 = 0.90$ and 0.88 , respectively).

Nitrogen and potassium were exceptions. Net photosynthetic rate declines as leaf nitrogen content increases. At a leaf nitrogen content of $15 \text{ mg g dry wt}^{-1}$ the photosynthetic rate predicted by regression analysis is $35 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ (Fig. 4). At a leaf nitrogen content of $20 \text{ mg g dry wt}^{-1}$ the photosynthetic rate has fallen by 31% to $24 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$. However, the large scatter in the data indicates that other factors may be involved in the depression of net photosynthesis at high nitrogen availability levels in addition to or instead of leaf nitrogen content. Potassium content increases with higher nitrogen treatment concentrations. Decreasing photosynthetic rates and respiration rates are also correlated with increasing potassium levels ($r = -0.6$ in each case). The reasons for this are not known. However, since nitrogen and phosphorus covary, it is not known if either is the causative agent for the decreased photosynthetic rate.

Root respiration showed a somewhat different pattern of nutrient effect. In general, root respiration rate increased as nitrogen concentration in the growth medium increased from 1 to 10 mM (Fig. 5). Above 10 mM, root respiration

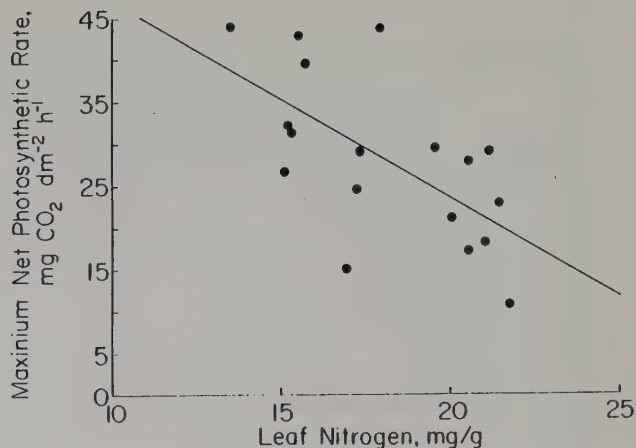


FIGURE 4. The relationship between leaf nitrogen content of plants grown under varying nutrient regimes and the corresponding maximum photosynthetic rate ($r = -0.64$, $R^2 = 0.41$).

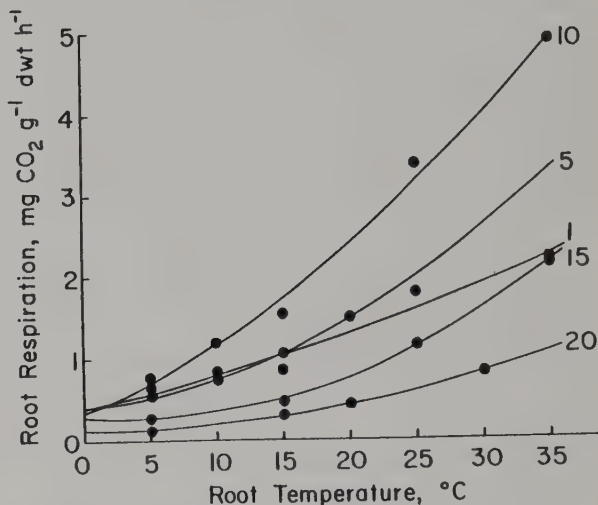


FIGURE 5. Temperature dependency of root respiration of plants grown under the five nitrate regimes. The numbers by each of the lines refer to nitrate treatment levels as mM nitrate. (r and R^2 values for nutrient treatments used are: 1 mM nitrate $r = 0.94$, $R^2 = 0.98$; 5 mM nitrate $r = 0.99$, $R^2 = 1.00$; 10 mM nitrate $r = 0.99$, $R^2 = 0.99$; and 15 mM nitrate $r = 0.97$, $R^2 = 0.99$).

rates fell as nitrogen concentration increased to 20 mM. The 20 mM nitrate treatment resulted in the lowest root respiration levels. The respiration rate predicted by regression analyses for roots grown at 1 mM nitrate is $1.1 \text{ mg CO}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$. At 10 mM nitrate this increases by 155% to $1.7 \text{ mg CO}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$. For plants grown at 20 mM,

the respiration rate is $0.3 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$, a value only 18% of that for plants grown at 10 mM nitrate. These differences among growth treatments may also be due to differences to maintenance respiration resulting from differential enzyme concentrations or protein turnover rates or they may be due to differences in growth respiration rates caused by differential growth rates and/or root turnover rates.

There is an inverse relationship between photosynthetic rate expressed as $\text{mg CO}_2 \text{ dm}^{-2}$ of leaf h^{-1} and total plant growth. The greatest growth rates are found under conditions where average maximum net photosynthetic rates are less than $20 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ (Fig. 6). The lowest above-ground growth was found where average maximum net photosynthetic rates averaged $31 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ and greater. Despite the apparent anomaly, greater plant growth rate is possible under conditions of decreasing photosynthetic rate if total canopy photosynthesis is higher at high nutrient concentrations due to increased allocation to leaf production resulting in greater leaf area. Increasing growth rates under conditions of declining photosynthetic rates have also been found under conditions of field fertilization in the arctic tundra (Bigger, Oechel, in press).

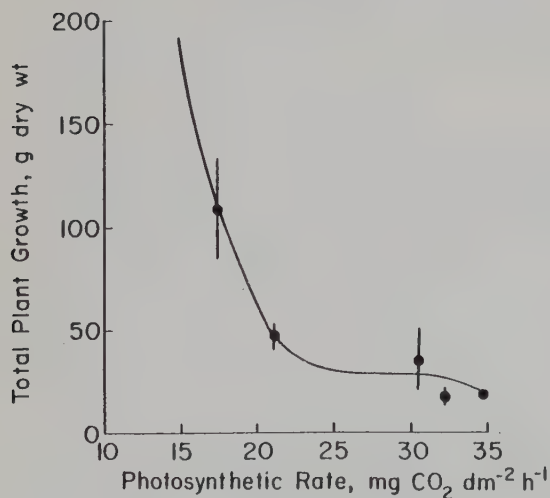


FIGURE 6. The relationship between measured photosynthetic rate and total growth per plant. Vertical bars = 1 SE of \bar{X} ($r = -0.90$).

To determine total canopy photosynthesis, photosynthesis on a dry weight basis was multiplied by the leaf weight of the plant measured. The results show that, despite decreasing photosynthetic rates (per unit leaf area or weight) at higher nutrient treatment concentrations, total canopy photosynthesis increases with increasing treatment nitrate concentration. The increased growth rates which were observed at nitrogen concentrations above 10 mM nitrate can be supported by increased canopy photosynthesis. The lowest calculated canopy uptake rates occur at the 5 mM nitrate treatment and were 79 mg h^{-1} (Fig. 7). Increasing the nitrate treatment levels from 5 mM nitrate to 20 mM resulted in a 300% increase in total canopy photosynthesis to $251 \text{ mg CO}_2 \text{ h}^{-1}$. The net carbon balance of the plants is further enhanced at elevated nitrate levels by the depressed respiration rates observed under these conditions.

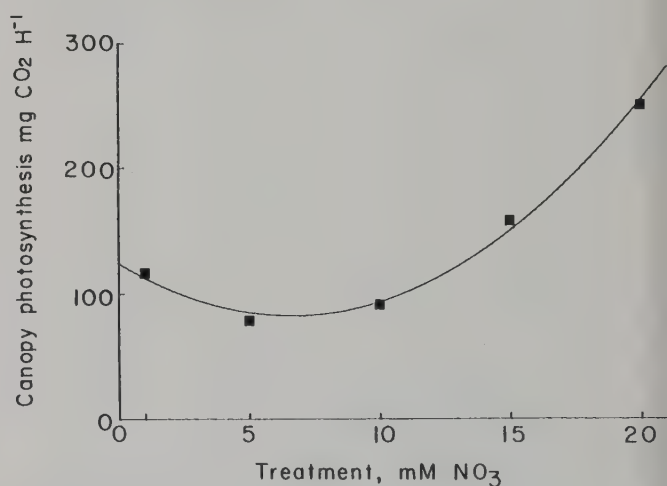


FIGURE 7. Total plant canopy photosynthesis at 25°C and $1600 \mu\text{E m}^{-2} \text{ s}^{-1}$ as affected by nutrient growth conditions ($r = 0.81$, $R^2 = 0.99$).

Calculating the effect of varying nitrate treatment levels on net CO_2 flux is complicated by the fact that varying levels of nitrate availability changes not only the rates of photosynthesis but also the rates of respiration and biomass production. Measured rates of photosynthesis and respiration were, therefore, coupled with measured biomass values to calculate average daily carbon uptake in

photosynthesis, loss in respiration, and net carbon accumulation in CO_2 equivalents. The calculations were necessarily simplistic, but the results serve as a useful comparison of carbon flux patterns among treatments. For each treatment and plant component measured (leaves, stems, and roots) CO_2 flux rates were multiplied by the measured biomass for each component. Total daily plant photosynthesis was calculated as the mean maximum net photosynthetic rate for 12 h times the measured leaf biomass. Daily leaf respiration was calculated at 15°C for 11 h. Daily root and stem respiration values were calculated at 15°C for 24 h. Leaf and stem respiration rates at 15°C were calculated from 25°C data assuming a Q_{10} of 2. Root respiration rates at 15°C were determined from the regression analyses presented in Fig. 5.

The results support the conclusion that on a whole plant basis there is more net carbon accumulation in the high nitrogen treatments than in the low nitrogen treatments despite the lower photosynthetic rates at these higher treatment levels (Table 1). The calculated net accumulation of carbon at 20 mM nitrate is more than twice the value at 10. Except for the 5 mM nitrate treatment, respiration accounted for between 52 and 61% of the net carbon assimilated. Photosynthate accumulation in biomass, therefore, ranged between 39 and 48% of the carbon uptake. This is higher than the value in mature chaparral, where a large standing biomass results in a higher percentage of carbon uptake being utilized for respiration (Oechel, Lawrence, 1980). The 5 mM treatment shows about 17% net CO_2 accumulation. This lower value is due, in part, to the unusually large respiring stem biomass at this treatment level. Despite the large differences in net CO_2 uptake between treatments, the plants from the various treatments (with the exception of the 5 mM nitrate treatment) were very similar in percent allocation of carbon to leaf, stem, and root respiration.

Leaf respiration utilized 30 to 37% of the carbon assimilated. Except for the 5 mM nitrate treatment which utilized 34% of the carbon assimilated for stem respiration, stem respiration utilized 8–20% of the carbon uptake. Root respiration utilized 6–12% of the net carbon available (19% for the 5 mM nitrate treatment). The greater utilization of carbon for maintenance of the stem and root compartments in the 5 mM nitrate treatment relative to the other treatments may reflect greater early growth of these structures which resulted in larger respiring biomass relative to carbon uptake potential.

The carbon allocation for *C. crassifolius* seedlings can be compared to the pattern of carbon allocation in mature shrubs growing in the field in California (Table 2). The mature field shrubs show a smaller allocation to leaf respiration of from 14–15% in *Arctostaphylos glauca* Lindl., *C. greggii*, and *Rhus ovata* Wats. to 30% in *A. fasciculatum*. Stem respiration is somewhat higher in the mature shrubs, reflecting the greater percentage of accumulated biomass as stem material. Stem respiration utilized from 14% of the net carbon assimilation in *A. fasciculatum* to 29% in *A. glauca*. Root respiration is also higher in the mature shrubs ranging from 11 to 27% of the net carbon assimilation. These higher respiration rates result in a lower net CO_2 uptake in the mature shrubs than was found for the *C. crassifolius* seedlings. Also indicated is the large expense associated with maintaining stem structures in mature vegetation.

The patterns of photosynthetic response to nutrient enhancement are different for nitrate enhancement in the laboratory than they are in the field following fire. In the latter case, increased nutrient availability following fire appears to result in increased photosynthetic rate. Perhaps the balanced addition of nutrient is important in maintaining elevated photosynthetic rates during enhanced growth rates. Variation of the concentration of a single element, nitrogen, may create new nutrient stresses within the plant.

TABLE 1. Calculated carbon budget for *Ceanothus crassifolius* receiving various nitrogen fertilizations. Respiration calculated for 24 h at 15°C except for leaves (11 h). Photosynthesis calculated as maximum photosynthesis for 12 h.

Treatment (mM NO ₃)	Leaf photosynthesis	Leaf respiration	Stem respiration	Root respiration	Net plant CO ₂ flux
		(mg CO ₂ day ⁻¹)		(% of total)	
1	1402	490 (35)	157 (11)	86 (6)	667 (48)
5	941	285 (30)	318 (34)	175 (19)	163 (17)
10	1093	353 (32)	138 (13)	127 (12)	475 (43)
15	1889	647 (34)	160 (8)	182 (10)	900 (48)
20	2988	1091 (37)	606 (20)	130 (4)	1161 (39)

TABLE 2. Simulated carbon budget (g CO₂ m⁻² year⁻¹) for four shrubs from Californian chaparral (modified from Oechel and Lawrence 1980).

Species	Net CO ₂ uptake	Leaf respiration	Stem respiration	Root respiration	Net plant CO ₂ flux
<i>Arctostaphylos glauca</i>	2116	300 (14)	615 (29)	429 (20)	772 (36)
<i>Adenostoma fasciculatum</i>	1784	638 (30)	291 (14)	232 (11)	622 (29)
<i>Ceanothus greggii</i>	1556	222 (14)	390 (25)	397 (26)	547 (35)
<i>Rhus ovata</i>	978	150 (15)	176 (18)	267 (27)	384 (39)

4. CONCLUSIONS

Increasing nitrogen levels between 1 and 20 mM nitrate causes a reduction in photosynthetic rate on a leaf area basis while allowing increased growth rates. Increased canopy leaf area and altered respiration rates result in increased canopy photosynthesis and increased net carbon assimilation by the plant despite depressed photosynthetic rates at higher nitrate treatment levels. The reason for the decreased photosynthetic rate in elevated nitrate treatment levels is not known, but may result from dilution of essential elements required in the photosynthetic process following increased growth.

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MIDDAY STOMATAL CLOSURE IN ARBUTUS UNEDO LEAVES: MEASUREMENTS WITH A STEADY-STATE POROMETER IN THE PORTUGUESE EVERGREEN SCRUB

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1. INTRODUCTION

General types of diurnal leaf stomatal behavior were described by Stocker (1956) who suggested an increasing degree of midday stomatal closure depending on the degree of water stress experienced by a plant. Initially the closure may restrict water use in such a manner that a single peaked curve is obtained for transpiration rate plotted against time, the changes in conductance at midday only nearly compensating for changes in evaporative demand and resulting in an approximately constant transpiration rate. The daily pattern of CO₂ exchange which is often directly affected by conductance changes may, under these conditions, reveal the stomatal closure response, and one observes two peaks in net photosynthesis rate. With further increase in plant water stress, Stocker suggested that extreme midday stomatal closure may affect the daily time course of water loss to such an extent that a two-peaked curve of transpiration rate versus time results, with a depression at midday.

Midday stomatal closure was interpreted as a feedback response to water loss which prevented further decrease in leaf water content. Recently, however, Farquhar (1978) pointed out that with a

feedback control mechanism as proposed by Stocker, an actual reduction of transpiration at midday with increasing evaporative demand can never occur, since closure immediately improves water status. At best a constant transpiration rate can be maintained. Extreme midday closure, on the other hand, may occur when stomata are controlled by external influences. One possibility, which has been proposed in interpreting midday closure of stomata of apricot leaves, is that stomata act as "humidity sensors" (Lange, 1969; Schulze et al., 1972) immediately changing conductance in response to a change in ambient evaporative conditions. Cowan and Farquhar (1977) have further demonstrated that such a "feed-forward" controlling system might enable plants to optimize water use efficiency or the daily amount of CO₂ fixed for a set quantity of water used.

As observed by Schulze et al. (1980) for plants growing under extreme conditions in the Negev Desert, the probability of midday closure does increase with seasonal increase in water stress. Similar though less extensive results were obtained for mediterranean plants in Chile by Mooney and Kummerow (1971) and in southern France by Eckardt et al. (1975). Probably the sensitivity of stomata to environmental factors, such as temperature and humidity, depends on the water stress experience of plants, and may be mediated by momentary stress as well.

Since plants growing in mediterranean climate regions of the world experience a

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prolonged dry season during which growth is water limited, a mechanism for optimizing water use efficiency would be potentially of great advantage. Although examples of midday stomatal closure in mediterranean type plants have been observed previously, e.g. with Lithraea caustica (Mooney and Dunn, 1970) in Chile, Heteromeles arbutifolia and Arbutus menziesii (Morrow and Mooney, 1974; Mooney et al., 1975) in California, or Quercus ilex (Eckardt et al., 1975) in France, an extensive study of midday closure reactions as related to internal plant water status and external environmental conditions, with the aim of determining the implications of such responses for seasonal water use and primary production, remains to be undertaken. This paper, describing the midday closure of stomata in Arbutus unedo and Quercus coccifera during the dry season in a macchia near Lisbon, Portugal, is an initial report from a program of study with four main objectives: first, to identify Mediterranean species in which midday stomatal closure importantly influences plant water and carbon dioxide exchange; second, to elaborate the mechanisms by which stomatal control is effected; third, to compare such plants with others that do not demonstrate midday closure behavior in the same environment; and finally, to interpret the ecological significance of the midday closure response, possibly from the standpoint of improved water use efficiency. The identification of plant species exhibiting midday closure, and also the possibility of assessing general characteristics of plant stomatal behavior, have been greatly facilitated by measurement of leaf resistance and

transpiration rate with a steady-state diffusion porometer (LiCor, Inc., Lincoln, Nebraska). With this apparatus, stomatal regulation of gas exchange of several leaves can be monitored throughout the day under almost natural conditions of light intensity, leaf temperature, and relative humidity.

2. METHODS

Daily time course measurements of leaf diffusion resistance, transpiration rate under porometer conditions, leaf temperature, and leaf microclimate were obtained from Arbutus unedo and Quercus coccifera leaves from plants of various ages and sizes in a macchia, or matorral formation, at the Biological Research Station Quinta São Pedro, Sobreda, Portugal in July of 1980. The macchia is of a type related to the order of the Quercetalia ilicis as described by Braun-Blanquet (1952) and is dominated by sclerophyllous species such as Quercus coccifera, Pistacia lentiscus, Phillyrea angustifolia, Arbutus unedo, Myrtus communis. The Atlantic character of this Mediterranean scrub as well as the low soil pH of the habitat is reflected by scattered Quercus suber trees and numerous Ulex parviflorus shrubs.

With the LI-1600 porometer, steady-state measurements of diffusion resistance and transpiration rate are obtained. After a set point for relative humidity of external air has been provided to the porometer controlling system, and a leaf is clamped into the porometer, the porometer automatically controls cuvette relative air humidity with a through-flow of dry air which compensates for leaf transpiration. At steady-state, the relative humidity in the cuvette and outside air are approximately the same. One can observe on the digital readout as

steady-state is approached and resistance and transpiration rate approach constant values (approximately 30 seconds). Each time it is decided that a steady-state transpiration rate has been reached, data values are stored in a memory and the leaf is removed. Experience suggests that this new porometer provides a more accurate picture of leaf behavior under natural conditions than previous porometer methods. The side of the leaf not being measured is freely exposed. Air temperature within the cuvette is held close to outside air temperature by radiation shielding and air ventilation. Therefore, leaf temperature is almost unchanged during measurement compared to natural conditions. Incident light intensity above the plant canopy and at individual leaves (PAR), relative humidity in the measurement cuvette, leaf diffusion resistance (lower surface - $s\text{ cm}^{-1}$), transpiration rate into the cuvette ($\mu\text{g H}_2\text{O cm}^{-2}\text{ s}^{-1}$), leaf temperature ($^{\circ}\text{C}$ - thermocouple), and air temperature in the measurement cuvette ($^{\circ}\text{C}$ - thermistor) were obtained directly from the LI-1600 steady-state porometer. Since the upper surface diffusion resistance for *Arbutus unedo* and *Quercus coccifera* is always high ($> 200\text{ s cm}^{-1}$), the lower surface resistances shown in Figs. 2 through 5 are also approximately equal to leaf diffusion resistances. The water concentration difference ($\text{WD} - \text{mg H}_2\text{O l}^{-1}$) between air saturation at leaf temperature and cuvette air temperature with measured relative humidity, was calculated and indicates evaporative demand to which the leaves were exposed during study. When averages of leaf resistance are presented, these averages are calculated as the inverse of average

leaf conductance values. The water potential of terminal shoots of the experimental plants was determined with a pressure chamber of the Scholander type (Scholander et al., 1965).

3. RESULTS

The month of July 1980 at the Quinta São Pedro in Sobreda, Portugal was extremely dry and the plants studied were under considerable water stress. Except for occasional days associated with passing weather fronts when wind and rapidly passing clouds were experienced, the sky remained clear and the daily time course of incident photosynthetically active radiation on the horizontal plane was similar to that shown for "light above canopy" in Fig. 1 measured on July 17. The curve shown is valid for incident PAR above the plant canopy on all days of measurement discussed below. Further curves in Fig. 1 will be referred to in the discussion of Fig. 5.

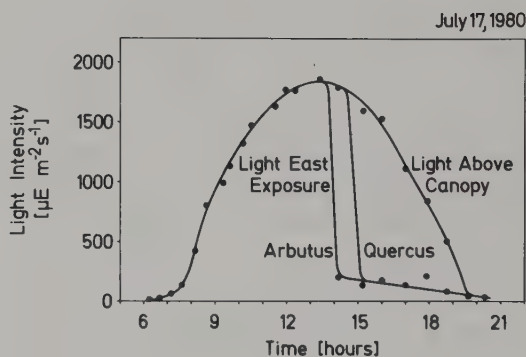


FIGURE 1. Measured daily time course of light intensity (PAR) above the canopy and near leaves of *Arbutus unedo* and *Quercus coccifera* (on the horizontal plane) on July 17, 1980. For further explanation of individual curves, see explanation of Fig. 5 in the text.

Shown in Fig. 2 are average responses measured for eight individual leaves of *Arbutus unedo* on July 13 and 14. In this case, the plant studied was a young plant that was well established in a small clearing in the macchia. Average above ground leaf height for these

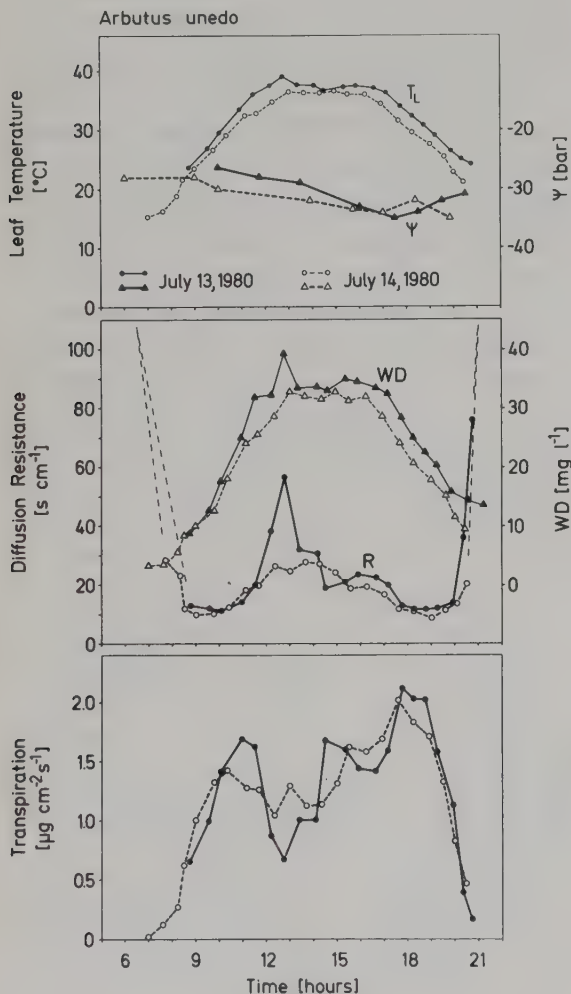


FIGURE 2. Daily time course of leaf temperature (T_L), plant water potential (ψ), leaf diffusion resistance (R), water concentration difference (WD), and transpiration rate measured for *Arbutus unedo* leaves on July 13 and 14, 1980 as described in the text. Average response for eight leaves.

leaves was 100 cm. The plant microclimate was strongly influenced by heating of the ground surface which raised air temperatures to between 35° and 40°C . Air temperatures between 30° and 32°C were recorded at most times in more turbulent air layers above the shrub canopy.

Leaf resistance (R) decreased rapidly in response to increasing light intensity and reached a minimum value of approximately 10 s cm^{-1} , when light incident on the horizontal plane was still quite low (100 to $200 \mu\text{E m}^{-2} \text{ s}^{-1}$). Due to the vertical orientation of leaves, light intensities on the leaf surfaces at this time were much higher than those given for the horizontal plane. This two to three hour period of relatively low resistance is undoubtedly used for significant CO_2 fixation. On both days of measurement, a pronounced midday increase in leaf resistance followed the period of early morning minimal resistance. July 13 was a slightly warmer day and leaf temperatures (T_L) were two or three degrees higher. The higher leaf temperatures together with a more rapid morning increase in leaf temperature on July 13, were apparently the cause of a much more extreme increase in leaf resistance, or degree of stomatal closure. Lower leaf temperatures in the afternoon apparently caused a re-opening of stomata, which continued until minimal values were again reached at 18 hours. Following a two hour period of relatively low resistance, rapid stomatal closure reoccurred in response to decreasing light intensity.

There is no doubt that *Arbutus* leaf resistance is strongly affected by leaf temperature. However, since the water concentration difference (WD) between leaf and air simultaneously changes with leaf temperature, an independent effect of humidity or

water concentration difference on leaf resistance may occur. Changes in leaf resistance may be the result of a direct temperature effect, a direct humidity effect, or both. Changes in WD are also indicated in Fig. 2. The strong correlation between T_L and WD is apparent. Also apparent is the strong correlation between leaf resistance and WD. On July 13, the initial extreme peak in leaf resistance and a second closing response after 14 hours are clearly associated with increases in T_L and WD.

While it cannot be said with certainty that the transpiration rate measured with the porometer is exactly the same as the transpiration which would occur with normal leaf boundary layer conditions, the results of Fig. 2 suggest that leaf resistance changes are large enough to result in a substantial depression of transpiration rate during midday even under natural conditions. Changes in boundary layer resistance as a result of cuvette ventilation cannot be large enough to mask this pattern in plant response. The strong reduction in transpiration rate results in little if any change in shoot water potential (ψ). Internal water potential changes, therefore, cannot be considered from these data to cause a hydroactive stomatal response.

An advantage of the porometer method is that the individual behavior of several leaves can be studied. The time course of leaf resistance and leaf temperature is shown for four individual leaves on July 13 in Fig. 3. From the time course of leaf resistance, one observes time periods when the leaves respond in a very homogeneous manner, e.g. during closure in response to light intensity.

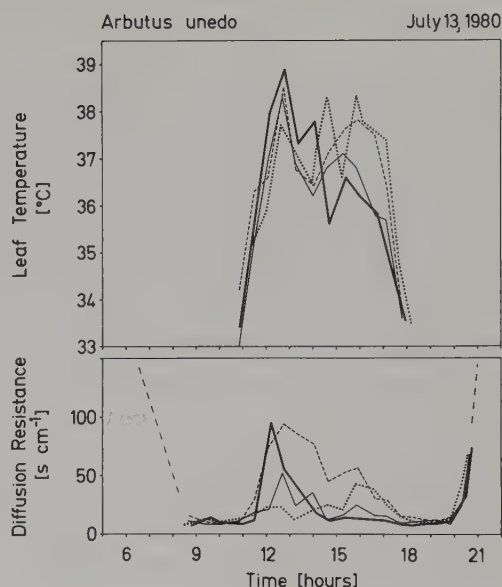


FIGURE 3. Daily time course of leaf temperature and leaf diffusion resistance measured for four individual leaves of *Arbutus unedo* on July 13, 1980.

During midday, however, an extremely heterogeneous response is seen. At any point in time, resistance in some leaves is increasing while in others it is decreasing or remaining constant. This heterogeneity can be explained as resulting from differences in leaf temperature which in turn result from differences in radiation incident on individual leaves and possibly small differences in air temperature. Almost all increases in individual leaf resistance are associated with increases in individual leaf temperatures, while decreases in leaf resistance are associated with decreases in leaf temperature. Exact correspondence between leaf temperatures and resistances should not be expected. Porometer measurements remain isolated point in time

measurements, while integrated temperature experience and associated changes in WD are decisive in determining leaf resistance.

Arbutus unedo reacted very sensitively to small changes in leaf temperature, especially above 33°C. Measurement of the temperature profile in the macchia suggested that air temperatures above two meters seldom exceed 30° to 32°C. Especially after noontime, fairly strong wind is common and is instrumental in maintaining relatively low air temperatures. The sharp reduction in leaf resistance occurring after 13 hours on July 13 (Fig. 3) was associated with sudden strong wind, which penetrated the plant canopy and lowered air temperatures (and thereby leaf temperatures) even at the 100 cm height. High sensitivity to leaf temperature changes is supported by data obtained from leaves situated at different heights in the macchia.

Leaves studied on July 22 (Fig. 4) were from a fairly large *Arbutus* tree which projected at least one and a half meters above the otherwise closed shrub canopy. Four leaves with a west exposure at 220 cm height were chosen, and also three leaves on the highest branches at 360 cm height. The results show that both sets of leaves exhibited similar behavior. Leaf resistance decreased as light intensity increased in the morning. Minimum resistance was slightly higher than on July 13 and 14, perhaps due to the extremely low water potential of this tree (approaching -40 bar). This minimum resistance was essentially maintained throughout the day. For a very short time around 14 hours, a tendency for resistance to increase was observed. This occurred when direct beam radiation

struck the leaves, resulting in an increase in leaf temperatures. Compared to the results shown in Fig. 2 and results presented below in Fig. 5, leaf temperatures and especially WD on July 22 were low.

In Fig. 5, results are shown for *Arbutus* leaves which are from the same tree as the leaves which were measured on July 22 (Fig. 4) but from the east side of the tree. Six leaves were measured at a lower average height of 135 cm. Six leaves of a shrubby

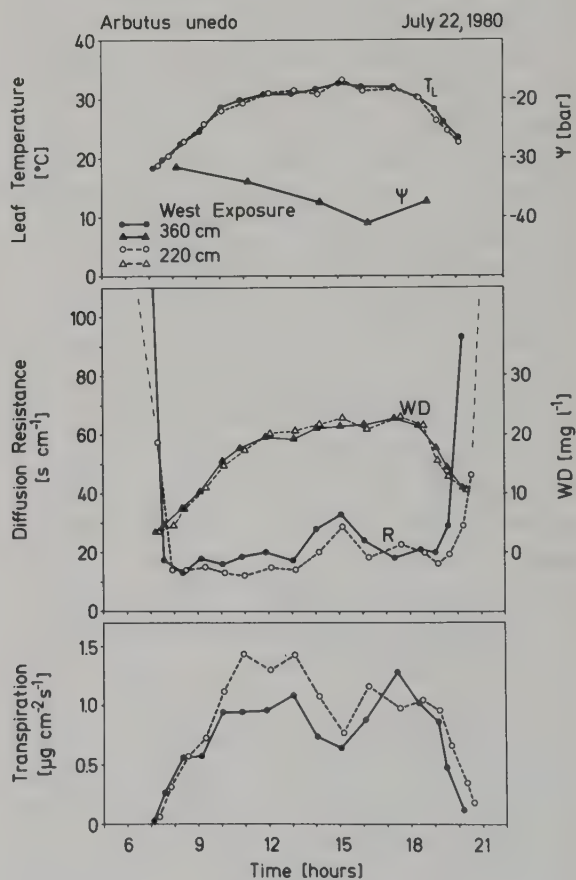


FIGURE 4. Daily time courses as in Fig. 2 measured for *Arbutus unedo* leaves at 220 cm and 360 cm height on July 22, 1980. Average response for four leaves at 220 cm and three leaves at 360 cm.

Quercus coccifera plant to the east of the Arbutus tree were also included in this experiment. Average leaf height of the Quercus leaves was 45 cm. As shown

in Fig. 1, the leaves were exposed to high light intensities until around 14 hours when the Arbutus canopy shaded first the Arbutus, and then the Quercus leaves. As seen in Fig. 5, Arbutus leaf resistance decreased rapidly in response to light intensity and reached the usual minimum resistance of around 8 s cm^{-1} . Leaf temperature and WD then increased rapidly. As leaf temperatures increased above 30°C after 10 hours, a rapid increase in leaf resistance occurred. Stomata partially reopened as leaf temperature and WD decreased during the afternoon. Low afternoon light intensities due to shading from the canopy may have contributed to the incomplete recovery of stomata.

The response observed in nearby Quercus coccifera leaves indicates that behavior of Quercus is similar to that of Arbutus. However, Quercus seems to open its stomata more slowly in the morning and begins closing stomata earlier. The minimum resistance attained appears to be slightly lower than that of Arbutus. A clear midday closure occurred although it was less pronounced than that observed in Arbutus. This may result from less direct sensitivity to temperature increases above 35°C and WD increases above 30 mg l^{-1} , or may be a result of a better water supply and different adjustment of internal plant modifiers of stomatal behavior. Water potential measurements indicate that the water supply is much better to Quercus (dawn water potential of -8 bar) than to Arbutus, allowing transpiration rates on a surface area basis that are almost double those of Arbutus unedo. The heating effect of the ground surface on leaf temperature is clearly seen in these data, where leaf temperatures of Quercus at 14:30 exceed those of Arbutus by 3°C even though transpiration rate appears to

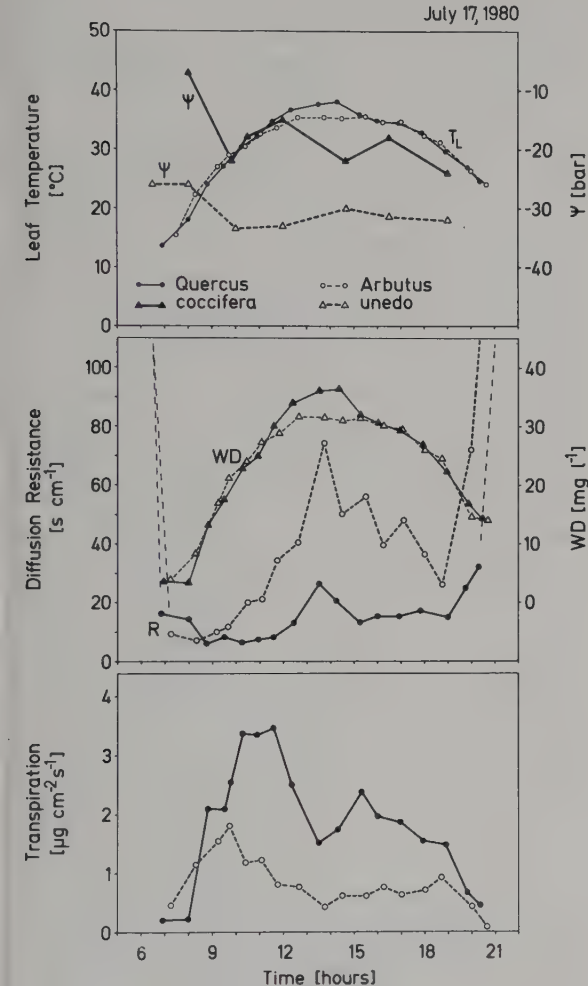


FIGURE 5. Daily time courses as Fig. 2 measured for Arbutus unedo leaves on the same tree as for results presented in Fig. 4. Average Arbutus leaf height was 135 cm; average response for six leaves. Daily time courses also shown for Quercus coccifera (6 leaves) at 50 cm height. Measurements on July 17, 1980 on the east side of a tall Arbutus unedo tree. Light intensity on the horizontal plane near the leaves studied is shown in Fig. 1.

be twice as high.

4. DISCUSSION

The results presented here, obtained with a steady-state porometer, indicate an extremely sensitive response of Arbutus stomata to either leaf temperature or air humidity (WD) or both. They also suggest that midday stomatal closure during long dry periods in the summer in Portugal is drastic enough to lead commonly to a midday depression of transpiration rate. The measured rate of transpiration into the porometer cup, however, is not necessarily the same as transpiration rate under natural conditions. On the other hand, considering the relatively high leaf resistances measured, changes in the boundary layer resistance are probably insignificant.

In an attempt to verify the results obtained in Portugal, studies of Arbutus unedo have been conducted in the Botanical Garden in Würzburg using cuvette gas exchange systems (unpublished). These studies confirm that for well-watered, potted plants of Arbutus grown outdoors under hot and dry conditions during the summer in Würzburg, a two-peaked daily time course is obtained for transpiration rate, even when leaf temperatures are moderate and vary between 30° and 35°C. The time course of photosynthesis rate is also two-peaked. With higher leaf temperatures, two periods of positive net photosynthesis, early and late in the day, occur. In these chamber experiments, stomatal response has also been found to be extremely temperature dependent. These additional results support the assumption that leaf behavior measured with the steady-state porometer accurately reflects natural behavior.

The midday depression of transpiration rate can be interpreted as a response directly controlled by an external factor. Alternatively or additionally, internal factors such as concentration of abscisic acid, with a time lag for production or removal, may play a controlling role. In these experiments, water potential did not appear to directly affect stomatal response. In the results presented and in the gas exchange experiments just mentioned, relatively little change in xylem water potential was measured between the time when stomata were fully open and when they were closed at midday. In the morning, light induced stomatal opening took place at xylem water potentials lower than -30 bars.

Arbutus unedo is an evergreen sclerophyllous shrub which possibly relies on midday stomatal closure to conserve scarce water resources during the dry season. At least this may be true during early stages of growth when leaves within one meter of the soil surface are heated to relatively high temperatures. The water stress experienced by Arbutus at this particular site was extreme. Compared to Quercus coccifera, Arbutus does not seem well suited to securing water under these extreme conditions. Water stress may be greater in small plants since they presumably have less storage capacity and may have less developed root systems but this cannot be judged from present information. The apparent success of Arbutus in this macchia suggests that the midday closure mechanism could importantly contribute to plant fitness and competitiveness. As plants age, the midday closure mechanism may become less important due to development of the root system, but also due to a lower evaporative demand accompanying lower temperatures experienced by leaves situated in colder air layers

above the shrub canopy.

Arbutus unedo is found naturally in what we can assume are a wide variety of habitats; dry sites such as described in this paper, Mediterranean montane regions, oceanic regions of northern Spain and southwestern France, and even naturally occurring in southwestern Ireland (Meusel et al., 1978; Good, 1947). It is reasonable that selective pressures on Arbutus unedo in regions with higher humidity and rainfall and with mild temperatures are very different, leading to races that are differentiated in leaf gas exchange function. If gas exchange of plants from such populations were to be compared under dry conditions to gas exchange of plants of populations adapted to extreme water stress, it might be possible to test whether "dry site" Arbutus is able to more efficiently use water resources in terms of carbon fixation and whether a tendency exists toward using water in an optimal fashion. A further survey of behavior of other species growing at the Quinta São Pedro site should reveal whether midday closure is characteristic of other *macchia* species.

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ANNUAL VARIATION OF PHOTOSYNTHESIS OF THE OLIVE TREE UNDER DIFFERENT WATERING CONDITIONS AND RELATED TO CHLOROPHYLL ACCUMULATION

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ABSTRACT

Olive trees were irrigated since planted either with drinking or with brackish water. The amount of irrigation applied covered 50%, 75% and 100% of potential evapotranspiration (PET at Tunis : 1400 mm; mean rainfall 450 mm). The results show that the olive tree has high photosynthetic capacity (compared with other species) but that it is rather affected by extreme watering conditions and by salinity. Excess of water (compared with needs) induces the same effects as lack of water or salinity and decreases photosynthetic capacity and chlorophyll accumulation. Nevertheless the effects of excess of water and salinity are not additive. Lack of water reduces photosynthesis more than does salinity. Also the effect of reduced irrigation on stomatal density is different of that of salinity.

The Olive tree possesses a seasonal rhythm of photosynthesis, depending mostly on temperature variation. Therefore assimilation drops during winter and grows quickly in spring with a small decrease by budbreak and after that a quick increase that coincides with fruit growth.

The annual rhythm of chlorophyll accumulation does not always coincide with CO₂ assimilation variations, however reduction of photosynthesis by salinity and low temperatures is partially linked with variations in the amount of chlorophyll, the variations of chlorophyll a being the most important.

1. INTRODUCTION

Water stress and salinity are known to affect photosynthetic rates. However the annual variation of these rates for perennial woody plants

under stress conditions have been little studied. This work concerns the analysis of those annual variations in the Olive tree (*Olea europaea*, L.) irrigated with drinking and brackish water. Chlorophyll content and stomatal densities were also determined.

2. MATERIAL AND METHODS

Two groves of Olive trees, cv "Chétoui", were planted in 1956 with a density of 6 m x 6 m, in the fields of the Water Studies Center at the Agronomic Institut of Tunis. One grove was irrigated with drinking water (from the Tunis city water supply) with 0.38 g l⁻¹ of dry residue. The other was irrigated with water from a deep well with a salt content attaining 3.5 g l⁻¹ dry residue in summer.

Irrigation was applied in complement of normal rainfall (annual mean 450 mm). Three irrigation levels were used, both with drinking and brackish water : level A corresponds to 100% of potential evapotranspiration (PET); level B to 75% PET and level C to 50% PET. Mean annual PET in Tunis amounts to 1400 mm. Each individual plot was formed of eight trees and each treatment was replicated three times.

Photosynthetic rate (PR) was measured in detached twigs rehydrated previously overnight and allowed to dry out while the measurements were made using an infrared gas analyzer (ANIR 12, Schlumberger). Chlorophyll content was determined according to McKinney (1941) modified by Mousseau (1969). Stomatal density was measured with an Ultropak microscope with a micrometric objectif, after fixation in alcohol glycerol.

Water and osmotic potentials were obtained using the microspectrometric method of Spanner (1951)

with a Wescor instrument.

3. RESULTS AND DISCUSSION

Crop yields from these experiments have already been published elsewhere (Vernet et al., 1964; Ben Mechlia, 1974; Laouar, 1977) : it was observed that the water requirements of the Olive tree for full productivity were moderate (60 to 65% of PET under Tunis conditions) and that irrigation to 100% PET decreases production of olives and oil (drinking water) or only of oil (brackish water). Furthermore moderate irrigation increases yield severalfold compared with dryland groves. Osmotic adjustment of leaf tissue seems to be very good (Laouar, 1977).

3.1. Evolution of assimilation rate as a function of leaf water content and irrigation treatment

Net photosynthetic rates measured in June, when the biological activity of the plant is at a maximum, show that the highest rates do not occur at the maximum leaf water content (fig.1), but only at less than 90% of relative water content (TR).

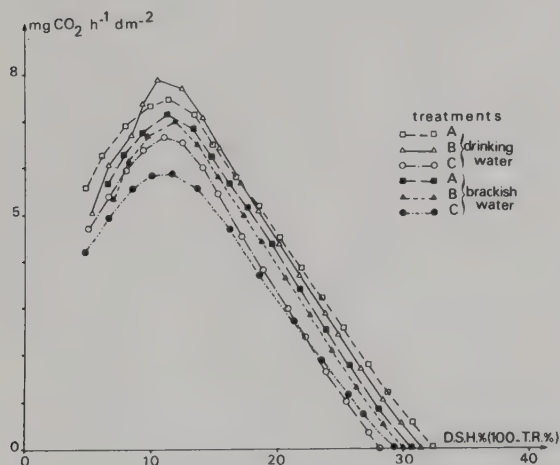


FIGURE 1. Photosynthetic rates at different leaf water contents.

This maximum has been supposed to correspond to maximum stomatal opening (Glinka, 1971) even if mesophyll resistance and chloroplastic biochemical activities are probably involved.

The curves for PR give lower intensities with increased salt and water stresses (fig. 1). The same result is observed with the annual means of maximum activity (fig. 2).

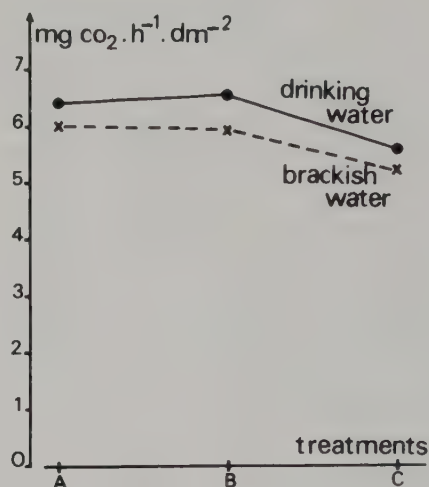


FIGURE 2. Photosynthetic rates under different irrigation treatments.

Maximum photosynthesis decreases in the following order : B drinking (Bd); Ad; A brackish (Ab); Cd and Cb. This rating is identical with that observed in yield results, with water adjustment in leaf tissue, and with ratings of organelles integrity observed by electron microscopy (Laouar, 1977). Similar results were obtained with other plants by Shimshi (1963), Boyer (1965) and Laouar (1973). After the maximum has been obtained, the progressive drying of Olive leaves reduces PR for all treatments, as it has been observed by Larcher (1961a, 1963) with detached twigs of Oak and Olive. Nevertheless there is no correspondance between the effect of different treatments and stomata density (fig. 3).

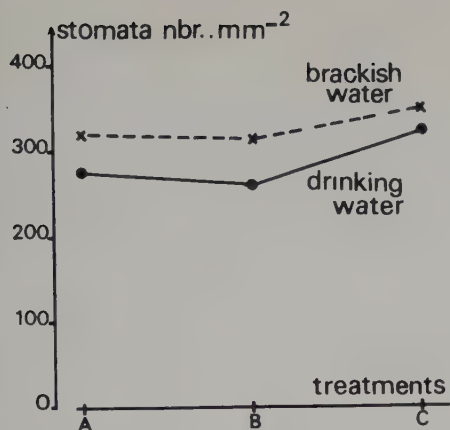


FIGURE 3. Number of stomata under different irrigation treatments.

PR is nul for water deficits (DSH) of about 30% of maximum water capacity (fig. 1), with small differences according to the treatments. Those values are higher than those obtained by Larcher (1975) : 22%.

3.2. Annual variation of PR in relation to chlorophyll content

The photosynthetic activity of the Olive tree can be observed during most of the year if environmental conditions are favorable. Temperature and evapotranspiration seem the most important factors affecting PR, and even if Larcher (1975) shows that the Olive tree has no frost tolerance (-10°C minimum temperature), this temperature level is of no interest under Tunisian conditions.

A well marked seasonal rhythm in PR can be observed in the Olive (fig. 4 and 5). The minimum of PR by the end of December is linked with low temperatures and low physiological activity. Another low point can be observed at bud break in March followed by a rise of PR after flowering till the end of July, when a decrease seems linked with a decrease in biological ac-

tivity by late summer, that cannot be relieved by irrigation. The growing of fruits correspond to another period of high PR in autumn and early winter. The observations confirm the results of Larcher (1964) obtained under more temperate conditions in northern Italy.

In Tunisia the annual variations of PR seem to be linked with chlorophyll content (fig. 6) except for the March minimum and for the autumn maximum, the first being the result of bud break without any effect in the amount of chlorophyll and the second being the effect of the fruit sink on photosynthesis, even if chlorophyll is decreasing. On the whole, the effects of salt, too much or too little water and low and high temperatures, are more important in chlorophyll a content than in chlorophyll b. In spring new synthesis of chlorophyll a increases the ratio a/b.

4. CONCLUSION

The Olive tree has a relatively high PR compared with other woody species, but it is also somewhat affected by extreme water conditions and by salinity. Too much water can give results similar with those of lack of water and salinity decreases also PR and chlorophyll content. Nevertheless salinity seems to give some compensation to slight water stress.

The seasonal rhythm of PR depends on internal factors and on the evolution of environmental conditions, mostly temperature. The seasonal rhythm of chlorophyll content however is not linked with that of PR even if the reduction of PR by low temperatures and salinity is linked with a decrease in chlorophyll a content.

The Olive tree shows a good adaptation to mediterranean climate with a rest during late summer. Irrigation does not seem to be useful outside the periods of high biological activity : end of spring and early summer and autumn and brackish water can be used in moderate amounts without

ADAPTIVE RESPONSES OF LEAF WATER POTENTIAL, CO₂-GAS EXCHANGE AND WATER USE EFFICIENCY OF *OLEA EUROPAEA* DURING DRYING AND REWATERING

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1. INTRODUCTION

The characteristic eco-physiological feature of sclerophyllous Mediterranean plants may be summarized as the ability to maintain sufficient metabolic activity and productivity in an environment which two unfavourable seasons: a period of drought during summer and early autumn, and short periods of low temperatures in winter. The ability of evergreen plants to tolerate dry seasons must include sufficient drought resistance and certain adaptive mechanisms, which enable the plants to remain productive when water resources are reduced. The resistance of Mediterranean sclerophylls to lethal desiccation has been studied by Oppenheimer (1932), Rouschal (1938), Oppenheimer, Leshem (1966), and responsive increase in desiccation resistance of olive leaves during summer drought was shown by Larcher (1963a). Concurrent measurements of water relations and CO₂-gas exchange of sclerophyllous plants have been carried out in the Mediterranean region (France: Killian 1933, Eckardt et al. 1975, Italy: Weinmann, Kreeb 1975), with species native to California and Chile (Mooney et al. 1975, Dunn 1975, Gigon 1979), and in Australia (Hellmuth 1971). However, a thorough analysis of the components of drought adaptation in the metabolism and dry matter production of sclerophyllous Mediterranean trees has still to be done.

The preliminary study presented here is intended as a conceptual approach to a synoptic view on the interrelated effects of drought stress and drought conditioning on water relations and CO₂-gas exchange of *Olea europaea*.

2. METHODS

2.1. Drying procedure

Potted trees of *Olea europaea* L. cv. Leccino, 22 years old and 1.8 - 2 m tall, were subjected in the laboratory to three consecutive drying and rewatering cycles. Before starting the experiments the plants were brought to full turgidity by watering the soil (container volume: 50 l) and by covering the shoots with plastic bags. During slow drying, CO₂-gas exchange and transpirational water vapour flux from twigs enclosed in ventilated sample chambers were continuously measured, and the water status of representative twigs was determined at 11 a.m., 3 and 6 p.m. every day. Water was withheld until CO₂-uptake was no longer detectable; this was the case after 7 - 8 days. Immediately after complete cessation of apparent photosynthesis, the pots were rewatered to full soil capacity. When the leaves had regained turgidity, watering was suspended in order to start the next drying cycle. Since stomatal reactivity requires more time for recovery than water saturation of leaf tissues (cf. Loveys, Kriedemann 1973, Kramer, Kozlowski 1979), photosynthesis and transpirational flux were not restored to the pre-stress level before starting the next drying cycle.

2.2. Measurements

Leaf water status: Water saturation deficit (WSD) was determined by weighing leaf samples after detachment and again after 2 d resaturation between wet filter paper. WSD is expressed as percentage of saturation water content; it can be converted to relative water content (RWC) by the relation $RWC(\%) = 100 - WSD(\%)$. The total leaf water potential (Ψ) was measured with single leaves (3 - 5 replicates) using

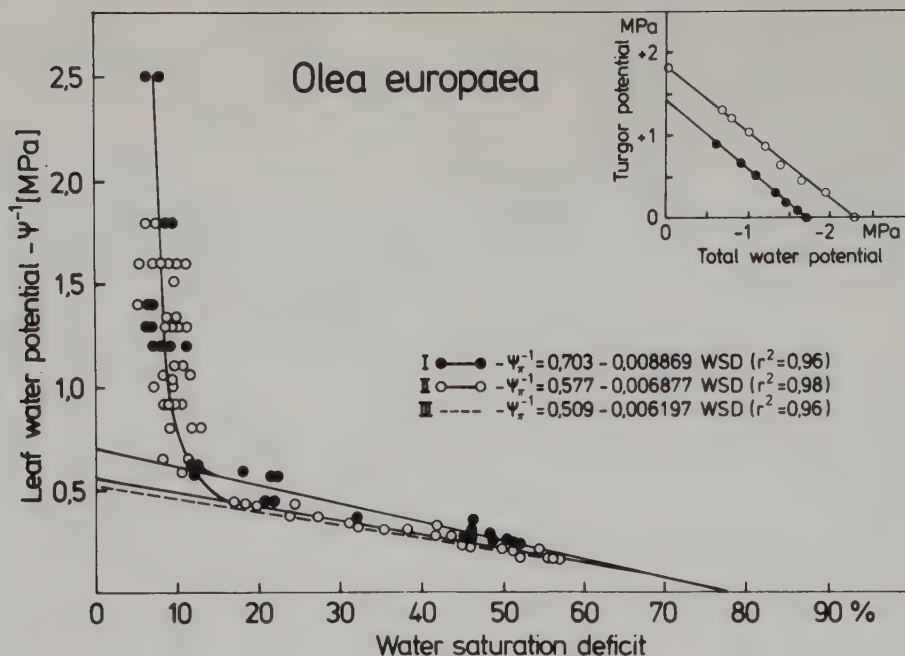


FIGURE 2. Water status plot for olive leaves during drying cycle I, II, and III. The regression line indicates the dependence of osmotic potential (Ψ_{π}) on relative water saturation deficit; at the intersection with the ordinate (full turgor point) the extent of osmotic adjustment becomes evident. The zero turgor point corresponds to the water potential where the pressure curve deviates from the regression lines. Inset: Turgor potential in dependence on total leaf water potential during the 1st (dots) and the 2nd drying cycle (circles).

Turner 1980, Kandiko et al. 1980, Cutler et al. 1980a, b). The adaptive effect of slow and progressive drying on leaf tissue water status of *Olea europaea* was assessed from the WSD/Ψ^{-1} -plots in Fig. 2. After drought stress, i.e. just at the end of the second drying cycle, the osmotic potential at full turgor was decreased by 0.4 MPa (28 % of the initial value -1.42 MPa), at the end of the three drying cycles by 0.55 MPa (39 % of the initial value). The leaf water potential at zero turgor was -1.65 MPa in the first drying cycle and -2.22 MPa after drought conditioning. The chemical basis of the osmoregulative response to drought in *Olea* has not been determined, but observations of Thomaser (1975, see Larcher 1980: 141) on mature trees in northern Italy during summer drought suggest stress dependent conversion of starch to sugars as a possible mechanism.

3.2. CO_2 -Gas exchange

As shown in Fig. 1, with increasing WSD, photosynthesis attained more than 80 % of capacity as long as turgor potential remained above zero. When water potential fell below turgor loss point, CO_2 -uptake was drastically reduced to 10 % of capacity within 3 days. After two more days F_n became nil. After rewatering, both photosynthesis and transpiration recovered quickly to about 50 % of capacity but more slowly to the final peak level.

Dark respiration was enhanced during desiccation one day after turgor became zero by a factor of 1.2 times the normal rate (from 0.6 to 0.7 $\text{mg CO}_2 \text{ dm}^{-2} \cdot \text{h}^{-1}$) and during recovery of turgor by a factor of 1.5. At water potentials below -4 MPa dark respiration was less than 0.55 $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$. The respiratory rise can be interpreted as a mitochondrial stress reaction (cf. Stålfelt 1937; Schneider, Childers 1941; Montfort, Hahn 1950; Stocker 1948, 1956: "Reaktions-

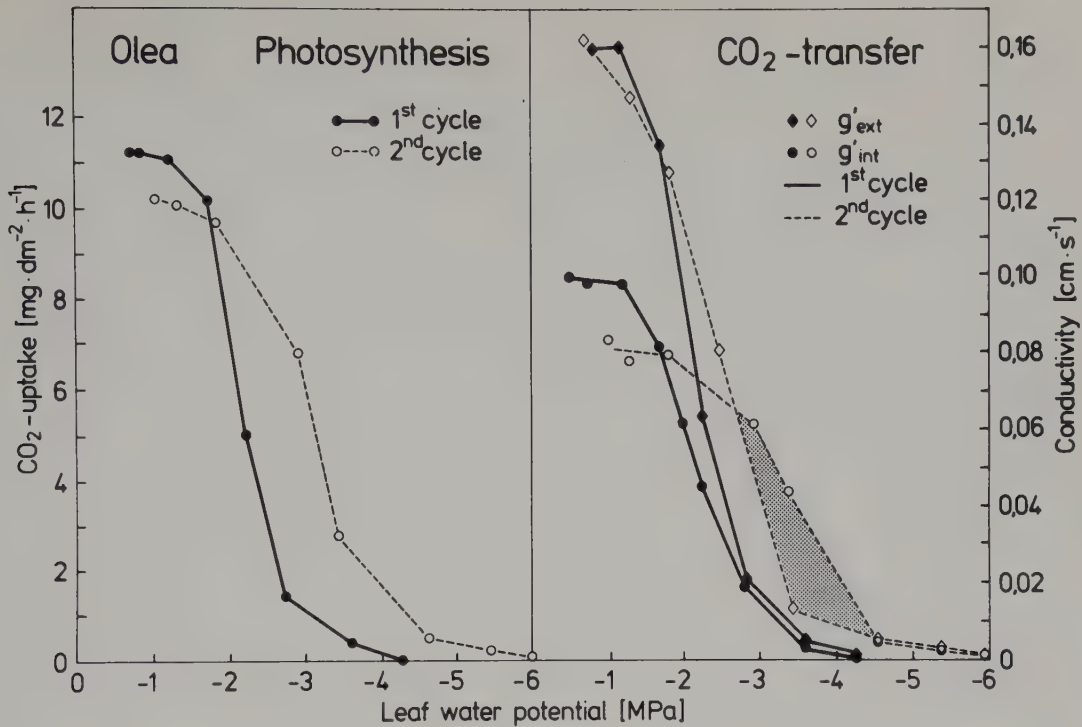


FIGURE 3. Net photosynthesis, and extracellular (g'_{ext}) and intracellular (g'_{int}) transfer conductances for CO₂ of olive leaves during slow drying. The shaded area indicates the range where g'_{int} remains effective while g'_{ext} limits the CO₂-uptake.

phase") or as a consequence of the accumulation of glycolysis products due to reduced mitochondrial activity during the time of strong desiccation.

The adaptive result of drought stress on CO₂-uptake is shown in Fig. 3: F_n of non-adapted leaves in the 1st drying cycle began to decrease below -1.3 MPa, it was reduced to 50% of capacity at -2.2 MPa, and to zero at -4.3 MPa. In the 2nd and 3rd cycles more than 50% of capacity was maintained at water potentials above -3.1 MPa, and CO₂-uptake was completely inhibited only when -6 MPa was reached. The adaption effect is attributed to a diminished susceptibility of the photosynthetic processes to drought stress at the cellular level. Before and during the first stress event g'_{int} remains lower than g'_{ext} thus limiting the CO₂-uptake. In contrast, after drought conditioning, g'_{int} decreases much more slowly with developing WSD than

g'_{ext} , which limits CO₂-transfer below -2.7 MPa in the 2nd cycle and during nearly the whole 3rd cycle.

3. Water use efficiency

As expected from the pronounced adaptive shift of g'_{int} water use efficiency tended to improve with progressive drought stress and drought conditioning (see Fig. 1). A small increase in ω_r occurred at narrowed stomatal apertures at the end of the 1st dying cycle and at the beginning of recovery after rewetting. In the consecutive drying cycles 1 - 2 days after turgor loss very high values of ω_r were attained. At this stage F_n rates were still 3 - 5 mg CO₂ dm⁻² h⁻¹ (30 - 45% of the initial photosynthetic capacity).

Similar increases have been observed in ω_F (the ratio of photosynthesis to transpiration) during the stomatal closure phase at desiccation with detached twigs of *Quercus ilex* (Larcher 1960), with intact shoots of *Olea europaea* (Larcher 1963b), and by Müllerstael

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SOME ADAPTATIVE PHOTOSYNTHETIC CHARACTERISTICS OF A SUN PLANT (*CERATONIA SILIQUA*) AND A SHADE PLANT (*COFFEA ARABICA*)

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1. INTRODUCTION

In previous experiments the effect of CO₂ concentration in the air, light, temperature and soil water content in stomatal resistance of *Ceratonía siliqua* has been evaluated (Nunes, Correia 1980 and Nunes, Linskens 1980). Both the anatomical features of the leaf as well as the stomatal behaviour against the main environmental factors compose the classical picture of a sun loving, heat and drought tolerant plant, as is due to evergreens adapted to the mediterranean climate.

Although some data had been obtained by Correia, Catarino (1978) concerning O₂ uptake of leaf discs at different temperatures, the effective carbon assimilation rates had not been measured in the intact leaf.

The present work contributes to fill in this gap. *Coffea arabica*, another evergreen plant which grows spontaneously under the shade in tropical and sub-tropical areas, is used as a contrasting example.

2. MATERIAL

Plants about three years old grown in pots under natural light and temperature in a greenhouse have been used. Some measurements were made in Nov./Dec. (exp. I), other in Feb./Mar. (Exp. II). During the intermission period the plants were fertilized and kept in a semi controlled room (20°C average day/night temperature) with artificial light. The leaves that were measured had matured under the previous green-house conditions.

3. RESULTS

3.1. Light dependence of photosynthesis

Net photosynthesis was measured under normal

atmospheric conditions by infrared gas analysis. As shown in Fig. 1 the curves from the two plants were different in a) the absolute rate at low levels of light and b) the irradiance saturating photosynthesis.

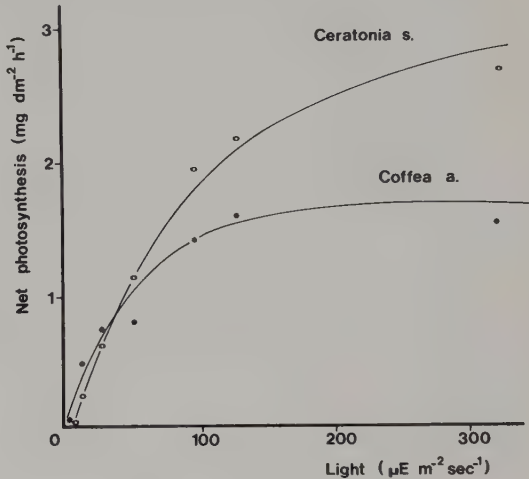


FIGURE 1. Net photosynthesis of attached leaves at 24°C against incident light flux density. Each point is the average of four measurements in different plants.

Coffea showed the double of the *Ceratonia* rates under 6 μE m⁻².sec.⁻¹. Under this low light *Coffea* photosynthesis was reduced to about 1/3 of its maximum and *Ceratonia* to less than 1/10. *Coffea* was saturated at 120 μE m⁻² sec.⁻¹.

Although the absolute rates were rather low, the response to light was typical of a shade and a sun plant and agree with previous results of one of the authors in *Coffea* (Nunes, et al, 1968).

3.2. Quantum requirement

The efficiency of the photochemical process can be appreciated by the slope of the light-photosynthesis curve close to the compensation point.

consumption being evaluated in a close circuit. This method allowed the determination of the CO_2 compensation points and the relationship of rates with CO_2 concentration in the air. The mesophyll resistance was also calculated from the slope of the linear portion of these curves (from 300 to 200 v.p.m.) according to the method of Holmgren et al., 1965.

Fig. 5 shows that photosynthesis rate at low temperature decreased both in *Ceratonia* and in *Coffea*. Table II shows the changes in CO_2 compensation point, stomatal and mesophyll resistances in the same experiments of Fig. 5.

Assuming the physical mode Gaasstra (1959) for photosynthesis, the decrease in rate due to low temperature is explained by the increase stomatal plus mesophyll resistances in *Coffea* but only by stomatal control in *Ceratonia*.

TABLE II. Effect of temperature on resistances (sec.cm^{-1}) to CO_2 transfer (stomatal resistance r_s , mesophyll resistances r_m) and CO_2 compensation point. Boundary layer resistance reported to one leaf surface was $r_a=3$ in *Coffea* and $r_a=2.6$ in *Ceratonia*, as measured by evaporation of a water saturated filter paper replica. The values are the average of four leaves from different plants under $320 \mu\text{E m}^{-2}\text{sec}^{-1}$ of irradiance (exp. II).

Temp. (°C)	<i>Coffea</i>				<i>Ceratonia</i>			
	r_{total}	$1.6(r_s+r_a)$	r_m	C.P.	r_{total}	$1.6(r_s+r_a)$	r_m	C.P.
10	59.5	24	35.5	60	59.5	45.8	13.7	60
24	23.8	14.4	9.4	60	23.8	4.1	17.2	60
34	178.6	+53	+125	130	22.6	5.2	17.5	80

The depressive effect of high temperature in *Coffea* is due to the increase in the compensation point. Although this parameter did also present a 25% increase in *Ceratonia* it merely leads to a small change in the gradient (less than 10%), the overall effect of the diffusion equation being compensated by the decrease in stomatal resistance. We can not explain why the rates obtained in the two sets of experiments were different as well as some stomatal responses to the extreme temperatures under high light. The plants in November were in a phase of slow growth possibly because of seasonal transition and/or poor nutrition and/or acclimation. Recent results by O.L. Lange et al. (com. to the II Congress of F.E.S.P.P., 1980) show that

the photosynthetic capacity markedly change with season in several plants. They found that the optimum temperature for photosynthesis may shift towards lower or higher temperature or may flatten. Our results are not surprising if we think that *Coffea* and *Ceratonia* have flushes of growth that are probably linked to oscillations in photosynthetic rates. Considering the stomatal control there is also evidence for general plants and particularly for *Coffea* (reviewed by Kumar, 1979) that nitrogen and some cations can be modifiers of stomatal opening.

3.5. Relative photosynthetic performance of *Ceratonia* and *Coffea*.

Table III shows that the carbon assimilation of *Coffea* was higher than the assimilation of *Ceratonia* under low light except in two combinations

with moderate and high temperature. Under high light *Ceratonia* showed to be markedly more active than *Coffea*, as expected.

TABLE III. Relative rates of photosynthesis (*Ceratonia*/*Coffea*) at three different temperatures occurring either with low or high irradiance.

Temp. (°C)	Irradiance ($\mu\text{E m}^{-2}\text{sec}^{-1}$)			
	3.2 exp.I	24 exp.I	320 exp.I	320 exp.II
10	0.1	0.4	1.0	2.0
24	3.4	0.7	1.0	1.8
34	0.7	1.2	7.0	2.3

3.6. Water use efficiency.

A prediction of the carbon assimilated per unit of water transpired was made on the basis of the measured resistances involved in the CO_2 and H_2O

paths and CO_2 compensation point. The expression $P/T = (r_s + r_a)/r_m + 1.6 (r_s + r_a) \cdot (\Delta \text{CO}_2 / \Delta \text{H}_2\text{O})$ was used. Water vapour gradient was assumed constant.

TABLE IV. Water use efficiency (P/T) of plants under normal air CO_2 concentration at different temperatures. Values of r_s from Table I and r_{total} and CO_2 compensation point from Table II was taken as reference 100%

Temp. (°C)	P/T	
	Coffea	Ceratonia
10	67	280
24	100	100
34	35	75

The Table shows that 24°C is an optimum temperature for the productivity of water in *Coffea* whereas 10°C is the best for *Ceratonia*. Under high temperature this parameter had the lowest values for both plants. That means, that *Ceratonia* keeps assimilating carbon at 34°C with the expense of 25% more water.

Acknowledgement

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THE EFFECT OF SO₂ ON PHOTOSYNTHESIS AND STOMATAL BEHAVIOR OF MEDITERRANEAN-CLIMATE SHRUBS AND TREES

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1. INTRODUCTION

Air pollutants are known to have detrimental effects on the productivity of agricultural crops (e.g., Manning, Feder 1976) and native ecosystems (e.g., Miller, McBride 1975; Winner, Bewley 1978a,b; Winner et al. 1978; Kozlowski 1980) throughout the world. The vast majority of reports show that air pollutants decrease plant productivity. The few reports of stimulated growth due to air pollutants represent studies with agricultural crops (e.g., Bennett et al. 1974). Such growth stimulation of natural systems by air pollutants are not known to occur; but if they did would represent examples of eutrophication, which is a serious environmental problem usually associated with waterways.

Research on the effects of air pollutants on plants has accelerated greatly since the 1940's and is testimony to the fact that twentieth century industrialization has resulted in a steady increase in the rate of pollution emission. For example, global emissions of SO₂ have increased from 75 million tons per year in 1940 to a projected value of more than 175 million tons per year in 1980 (Bibbero, Young 1974). Current emission rates are high enough that ecologists and agriculturalists have come to recognize these effluents as environmental stresses with which plants must contend. In fact, recent studies show that pollutants are so pervasive in some locales that some ecotypes have developed resistance to industrial emission through natural selection (Taylor, Murdy 1975). In other cases, plant breeders have inadvertently developed pollution-resistant cultivars while attempting to increase crop production with stand and cross-pollination techniques (Bradshaw 1976).

The goal of most studies of the effects of air pollutants on plants is to define plant responses to pollutant doses. Plant responses commonly studied include fruit production, biomass production, and many physiological responses, including photosynthesis. Most of the recent advances in such studies involve increasing the sophistication of experimental control or enhancing techniques of detecting plant responses. To date there has been remarkably little effort directed towards studying the processes that govern the flux rates of pollutants from the air into leaves. These principles could be used 1) to estimate the quantity of pollutants a plant might absorb during a fumigation episode, 2) to forecast the effects of pollution absorption on metabolism, and 3) to predict the resistance ranking from an assemblage of species or cultivars. The research reported herein uses an ecological framework to interpret plant responses to SO₂ absorption. In addition, I will try to exploit fumigation studies with mediterranean-climate shrubs to outline one approach for predicting SO₂ impact on plants.

2. RESEARCH APPROACH

2.1. Mediterranean-climate plants: the pollution perspective.

The mediterranean-type climate is widespread throughout much of central and southern California. Air masses which are contaminated by emissions from cities on the coast are driven eastward by prevailing winds. As the air pollutants move inland, they eventually become trapped in valleys and basins ringed by mountains. Chaparral and coastal sage vegetation types are native to this climate zone. Chaparral shrubs are typically sclerophyllous evergreens, are deeply rooted, and are usually between 1 and 3 m tall. These plants commonly occur at high elevations, above 500 m to 900 m, in the North Coast ranges between San

Francisco and Baja California, and east to Arizona. The coastal sage shrubs are found at the drier, lower elevations of this range and are typically less than 2 m tall, are mesophyllitic, are drought-deciduous, and are shallow rooted. Recent studies have documented the effects of oxidants from automobiles and industry on stands in certain locales (Westman 1979). In addition, laboratory studies have documented the effects of precisely controlled SO_2 fumigations on photosynthesis and stomatal conductance of shrubs native to the mediterranean climatic zone (Winner, Mooney 1980a,b). Continued studies of air pollution effects on Californian evergreen and deciduous sage species will be necessary as air pollutants become an increasingly important environmental stress.

Evergreen and deciduous sage species have evolved a wide range of life-history strategies and physiological mechanisms for surviving the predictable seasonal drought which is characteristic of the mediterranean-type climates. For example, deciduous and evergreen life-history strategies represent contrasting adaptations for drought tolerance. Specific anatomical and physiological characteristics are associated with these strategies. Coastal sage species avoid drought by their deciduous nature. Their ephemeral leaves have rates of photosynthesis and transpiration that are higher than rates for evergreen species (Harrison et al. 1971). On the other hand, chaparral shrubs develop an adequate root system to ensure water for maintenance of leaves (which have low metabolic potential) throughout the year.

My approach to developing the capacity to predict the effects of SO_2 on plants involves monitoring the effects of SO_2 on the gas exchange characteristics of perennial evergreen and deciduous sage species. Since plants with contrasting intrinsic rates of photosynthesis

and transpiration can be expected to differ in SO_2 resistance, species that are native to the mediterranean-climatic zone should represent an array of metabolic responses to SO_2 . Thus, SO_2 -caused changes in metabolism can be interpreted in an ecological context and extended into a predictive framework.

2.2. Rationale of gas exchange experiments

Photosynthesis is very sensitive to SO_2 as well as to other air pollutants. Since CO_2 fixation is the driving force for biomass production, SO_2 -caused changes in photosynthesis are likely to be related to large-scale plant responses such as reduced growth rate or altered community structure. Although many methods accurately measure photosynthesis, the techniques of gas exchange provide a continuous and instantaneous view of the effects of SO_2 on CO_2 fixation rates. Cuvettes used in gas exchange systems often offer sophisticated control of environmental parameters; thus, modified leaf cuvettes make excellent fumigation chambers. In addition, careful manipulation of environmental parameters allows some diagnosis of the mode of SO_2 effects on photosynthesis.

Gas exchange experiments allow the effects of SO_2 on stomatal conductance to be monitored simultaneously with measurements of photosynthesis. Stomata regulate the flux rate of gases, including CO_2 and SO_2 , between the leaf and the air. Thus, measurements of conductance changes are related to changes both in photosynthesis and in the rate at which SO_2 is absorbed into leaf mesophyll tissues. Presumably, only SO_2 that diffuses through stomata and into leaf mesophyll can be directly related to SO_2 injury.

2.3. Review of previous fumigation experiments

My initial studies of SO_2 effects on plant metabolism of California shrubs have been limited to Dipylis aurantiacus, a drought-deciduous shrub, and to Heteromeles arbutifolia, an evergreen shrub. These

species are co-occurring in the mediterranean-climate zones of California, and they exhibit many of the anatomical and physiological characteristics associated with the deciduous and evergreen growth habits (Winner, Mooney 1980a). The drought-deciduous species had higher photosynthesis rates and conductance values than did the evergreen species. D. aurantiacus had (under optimal conditions) photosynthesis rates of $1.7 \text{ nmol CO}_2 \text{ cm}^{-2} \text{ s}^{-1}$, and water vapor conductance was about 10 mm s^{-1} . Photosynthesis of H. arbutifolia was $1.2 \text{ nmol CO}_2 \text{ cm}^{-2} \text{ s}^{-1}$, and water vapor conductance was 7.7 mm s^{-1} .

Fumigations at constant SO_2 concentrations between 0.2 ppm and 1.7 ppm lasted for 8 h and resulted in a continuous decline in transpiration rates, which indicates stomatal closure (Figs. 1A,B). The greatest decline occurred in the highest SO_2 concentrations. Stomatal closure during the exposure period resulted in a gradual reduction of SO_2 flux rates into the mesophyll tissues of both species.

Photosynthesis of both D. aurantiacus and H. arbutifolia also declined during 8 h periods of SO_2 exposure (Figs. 1C,D). The degree of photosynthetic decline was greatest at the highest SO_2 concentrations. SO_2 at 0.96 ppm reduced photosynthesis of D. aurantiacus to 40% of its rate in SO_2 -free air, while 1.71 ppm reduced the photosynthesis of H. arbutifolia to about 60% of the control value.

D. aurantiacus seemed to be the species that was more sensitive to SO_2 . SO_2 -caused photosynthetic decline for both species was attributed to stomatal closure as well as to injury to nonstomatal CO_2 fixation processes.

When H. arbutifolia and D. aurantiacus are fumigated at the same concentrations, the latter species absorbs more SO_2 through stomata

because it has higher conductance values (Winner, Mooney 1980b). By comparing experiments in which SO_2 absorption was equal for both species, it was apparent that D. aurantiacus was the more sensitive of the two species. These results suggest that plants with intrinsically high photosynthetic rates may be more vulnerable to SO_2 absorption than are plants with lower photosynthetic rates.

3. CURRENT RESEARCH: MATERIALS AND METHODS

3.1. Experimental plants

In order to develop a basis for generalizing the effects of SO_2 on the metabolism of mediterranean-climate shrubs, ten species were propagated for fumigation experiments. All of the species chosen are perennial shrubs common to either the chaparral or the coastal sage communities as well as one representative from the montane forest. All species are representative of either the evergreen or deciduous life history strategy. Specimens of Diplacus aurantiacus, Heteromeles arbutifolia, Salvia mellifera, Arctostaphylos densiflora, Ceanothus thyrsiflorus, Ceanothus maritimus, Quercus kelloggii, Quercus agrifolia, Ribes sanguineum, and Ribes viburnifolium were raised outdoors in pots. Experiments as described by Winner, Mooney (1980a,b) were completed between September and December, 1979.

3.2. The experimental system and protocol

The leaf area was determined for a single, intact leaf, and while still attached to the plant it was inserted into a flow-through cuvette. The cuvette was designed for monitoring flux rates of CO_2 , water vapor, and SO_2 between the leaf and air, as well as for monitoring and controlling environmental parameters (Winner, Mooney 1980a,b). After the leaf in the cuvette had attained a steady state rate of photosynthesis, SO_2 was continuously supplied to the cuvette at either 0.1 ppm, 0.2 ppm, or 0.5 ppm. The rates of photosynthesis and transpiration were monitored at intervals of about 1 h for the 8 h fumigation period. Since the leaf was the only SO_2 sink in the system, total SO_2

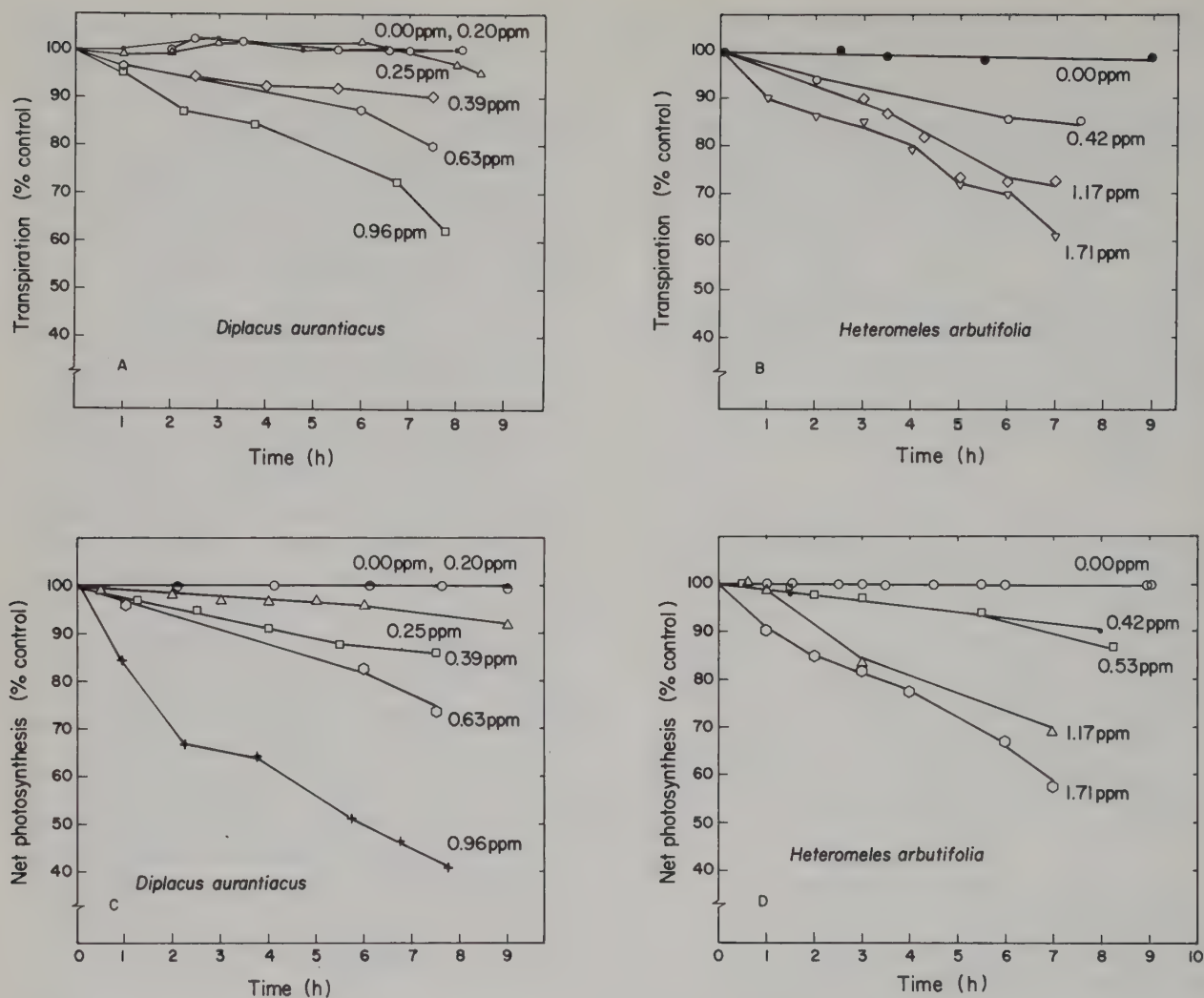


FIGURE 1. The time course of relative changes in transpiration (A,B) and photosynthesis (C,D) for *D. aurantiacus* and *H. arbutifolia* exposed to one of several SO_2 concentrations. Figures are modified from Winner, Mooney (1980a).

uptake by the leaf could be partitioned between adsorption to the leaf exterior and absorption through stomata. Environmental conditions were similar for all experiments: temperature was 20°C , PAR was $1200 \mu\text{E m}^{-2} \text{s}^{-1}$, vapor pressure deficit was 0.3 kPa to 0.7 kPa, and concentrations of CO_2 in the cuvette were maintained between 280 ppm and 200 ppm. Fresh leaf weight, dry leaf weight, and total nitrogen were

determined (by the Kjeldahl method) following the fumigation experiments.

4. CURRENT INVESTIGATIONS

4.1. Characterization of deciduous and evergreen shrubs

The data in Table 1 are representative of values obtained from analysis of several characteristics for each species. Although conductance values

TABLE 1. A list of deciduous and evergreen shrubs used in fumigation experiments. The leaves of each species are characterized by stomatal conductance values, specific weights, nitrogen content and photosynthesis rates.

Species List	J [*] _w mm·s ⁻¹	Leaf specific weight ^{**} g·m ⁻²	Nitrogen mg·g ⁻¹	Photosynthesis μmol·s ⁻¹		
				m ⁻²	g ⁻¹	gN ⁻¹
<u>Deciduous plants</u>						
Diplacus aurantiacus (Curtis) Jeps. ¹	6.3	63.1	26.6	19.7	0.31	11.7
Ribes sanguineum Pursh. ²	11.0	61.3	27.1	13.9	0.23	8.49
Ceanothus thyrsiflorus Esch. ^{2,3}	8.7	103	22.7	18.3	0.18	7.90
Salvia mellifera Greene ²	7.6	232	20.0	32.7	0.14	7.00
Quercus kelloggii Newb. ²	8.2	114	26.4	11.4	0.10	3.79
Mean (± S.E.)	8.4±.67	115±28	24.6±1.3	19.2±3.3	.19±.03	7.8±1.1
<u>Evergreen plants</u>						
Arctostaphylos densiflora M.S. Baker ²	7.5	282	10.3	16.1	0.06	5.43
Quercus agrifolia Neé. ²	4.1	162	16.5	10.6	0.07	4.24
Ceanothus maritimus Hoov. ²	8.4	230	16.8	15.8	0.07	4.17
Ribes viburnifolium Gray ²	5.6	161	17.2	11.0	0.07	4.07
Heteromeles arbutifolia (Ait.) Roem. ¹	4.9	186	21.7	12.0	0.06	2.95
Mean (± S.E.)	6.1±.72	204±21	16.5±1.6	13.1±1.1	.07±.002	4.3±.41

* J_w = Stomatal conductance for water vapor.

** All weights are on an oven-dried basis.

¹ Naming follows Thomas (1961).

² Naming follows Munz and Keck (1975).

³ This species is considered evergreen but produces many leaves which live less than one year (Munz, Keck 1975).

ranged from about 4 mm s⁻¹ to 11 mm s⁻¹, the group of deciduous species had a significantly higher mean conductance than did the evergreen species. These results are consistent with earlier reports (Harrison et al. 1971; Winner, Mooney 1980a). *D. aurantiacus* had the lowest conductance of the deciduous species; this value was also lower than were the conductance values for some of the evergreen species.

Photosynthesis, whether calculated on the basis of area, dry weight, or total N, was

significantly higher for the group of deciduous species than it was for the evergreen species. The higher photosynthesis of the deciduous shrubs was in part due to higher conductance. However, the group of evergreen shrubs had about 73% of the mean conductance of the deciduous shrubs but only about 68% of the photosynthesis (on an area basis). In addition, *D. aurantiacus* is known to have higher photosynthesis rates than *H. arbutifolia* on the basis of internal CO₂ partial pressures (Winner, Mooney 1980b). Thus, it seems that conductance differences between deciduous and evergreen shrubs

cannot fully explain differences between photosynthesis rates of these two groups.

The higher intrinsic photosynthetic capacity of deciduous shrubs may be related to specific leaf weights as well as to total N content. Evergreen leaves had more mass per area and less N per gram than did deciduous leaves. These data suggest that evergreen leaves have more nonphotosynthetic, structural tissue than do deciduous leaves. Greater density of the evergreen leaf type may increase leaf resistance to gas diffusion and might lead to water conservation (Slatyer 1964; Mooney, Dunn 1970; Harrison et al. 1971) and greater leaf longevity. In addition, higher N content of deciduous leaves may reflect greater concentrations of enzymes and greater metabolic potential of plant tissues. For example, Mooney et al. (1978) demonstrated that photosynthetic rates of Eucalyptus leaves are positively correlated with leaf nitrogen content.

4.2. Metabolic responses to SO₂ fumigations

Photosynthesis and conductance of both deciduous (Fig. 2) and evergreen (Fig. 3) plants were lower following 8 h of SO₂ exposure than they were when initially observed in SO₂-free air (the control value). Photosynthetic depression at the end of the fumigation was generally greater in the 0.5 ppm treatment than it was in the 0.1 ppm treatment. These patterns of metabolic response to SO₂ are similar to those observed for D. aurantiacus and H. arbutifolia (Figs. 1 A-D).

Three drought-deciduous species and three evergreen species had temporary increases in conductance when SO₂ concentrations were 0.1 ppm or 0.2 ppm. No increase in conductance was observed in the 0.5 ppm treatments. Conductance stimulation rarely exceeded 130% of control values and usually declined to

control values within 3 h of the fumigation period. A temporary increase in photosynthesis often accompanied the conductance stimulation.

The factors accounting for SO₂ stimulation of conductance are unclear. SO₂ stimulation of stomatal conductance was first reported for Vicia faba (Majernik, Mansfield 1970; Majernik, Mansfield 1972; Unsworth et al. 1972). Other fumigations of Vicia faba showed SO₂-caused stomatal closure at low relative humidities (Mansfield, Majernik 1970; Black, Unsworth 1980a,b). Thus, water vapor seemed to moderate the effects of SO₂ on stomata. Recent studies have shown that stomatal response of a species may also differ with respect to SO₂ concentrations (Winner, Mooney 1980c). Atriplex sabulosa was fumigated in high humidities (vapor pressure deficit less than 0.5 kPa). SO₂ treatments at less than 0.9 ppm resulted in temporary increases in conductance, whereas a treatment at 1.5 ppm resulted in a continual decline in conductance.

Stomatal responses to SO₂ are important for several reasons. SO₂ resistance of plants may be related in part to their ability to exclude SO₂ (Winner, Mooney 1980a,b,c; Black, Unsworth 1980c). For example, recent field studies have shown that Hawaiian plants that closed stomata in response to volcanic SO₂ appeared to have less foliar injury than did plants with stomata that remained open (Winner, Mooney 1980d). A secondary effect of SO₂ stress might be to stimulate conductance, thereby reducing the capacity of a plant to conserve water. Increased transpiration rates might be particularly detrimental to chaparral and coastal sage species which are adapted to water-limiting habitats.

4.3. SO₂ absorption into leaves: translating results into predictions

The difference between SO₂ concentrations entering and leaving the cuvette is due to SO₂ uptake by the leaf. Quantities of SO₂ uptake are related to leaf area, external leaf characteristics, and stomatal conductance. For example, the leaf of

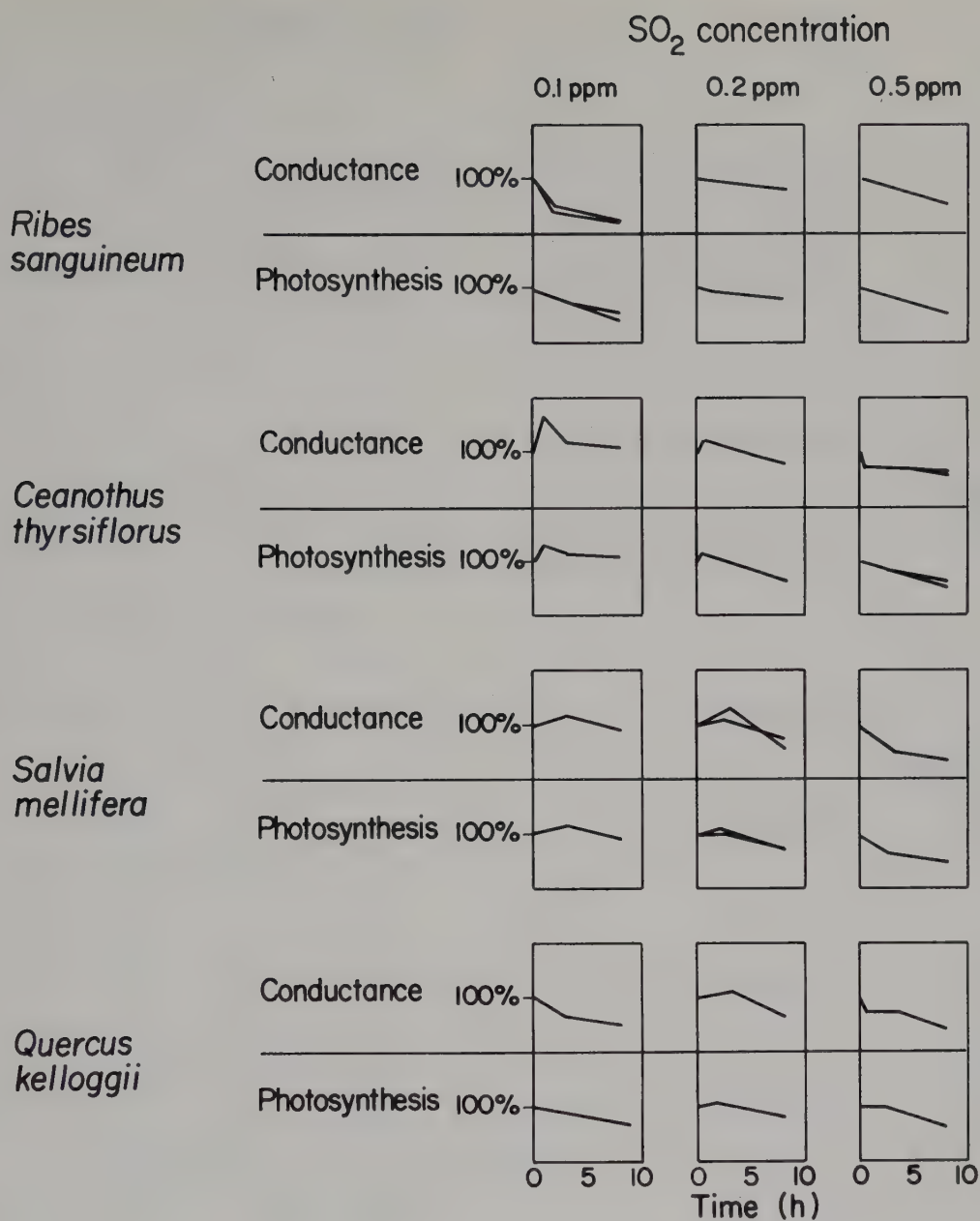


FIGURE 2. The effects of SO_2 exposures, at one of three concentrations during an 8-hr period, on relative photosynthesis and conductance of 4 deciduous, mediterranean-climate shrubs. Some experiments were duplicated.

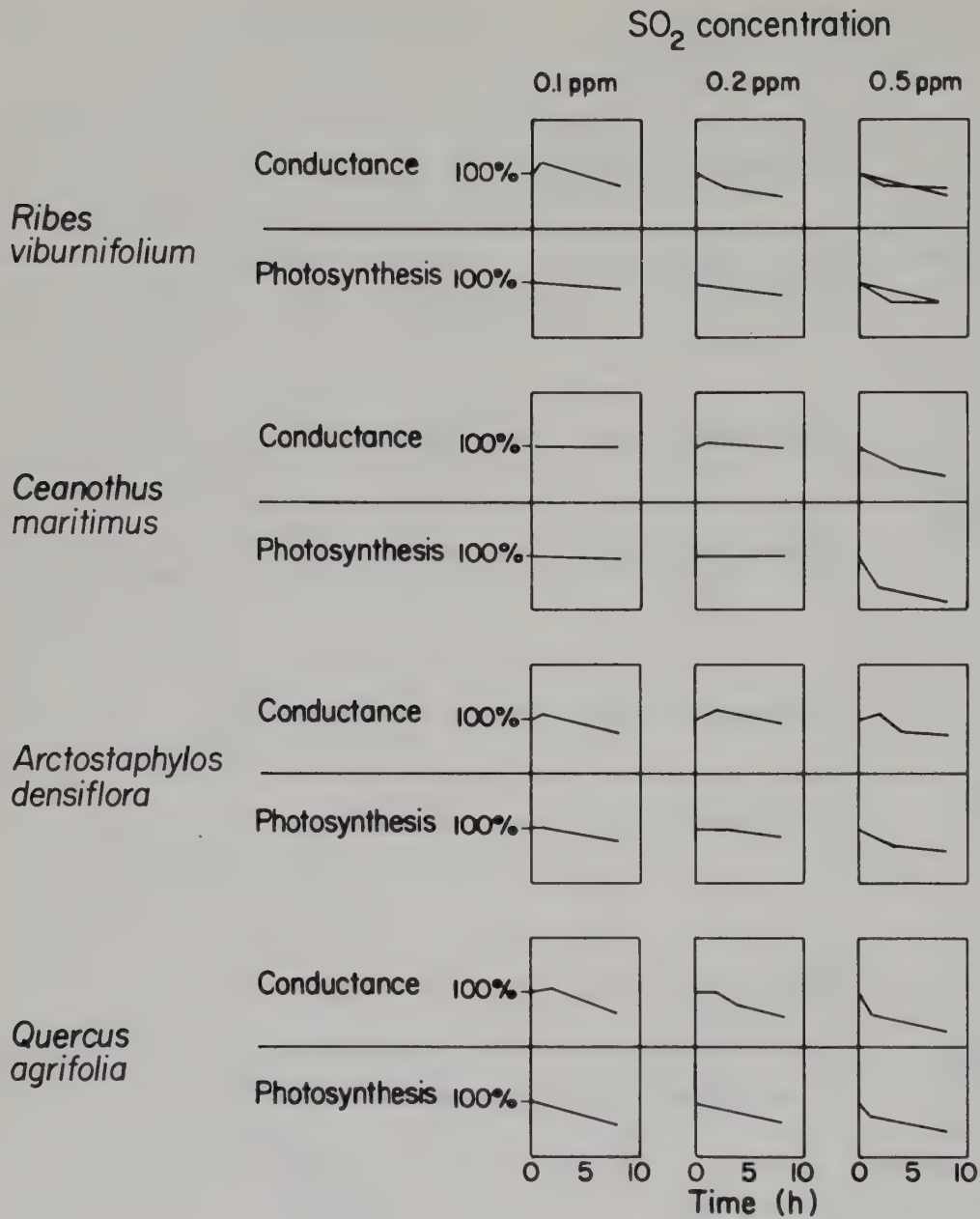


FIGURE 3. The effects of SO₂ exposures, at one of three concentrations during an 8 hr period, on relative photosynthesis and conductance of 4 evergreen, mediterranean-climate shrubs. Some experiments were duplicated.

D. aurantiacus is hairy, glandular, and covered with phenolic resins (Lincoln, in press). On an area basis it has at least twice the capacity for SO_2 absorption as was measured for the glabrous leaf of H. arbutifolia (Winner, Mooney 1980b). The extent to which SO_2 concentrations are depleted by foliar absorption is important because the SO_2 concentration leaving the cuvette is assumed to be the concentration around the leaf. SO_2 concentrations leaving the cuvette and stomatal conductance values can be used to calculate SO_2 flux rates (Winner, Mooney 1980a,b). Leaves with high adsorption rates can effectively reduce ambient SO_2 concentrations in the cuvette of the fumigation system at Stanford University by as much as 50%. Whether the hairs, glands, and resins generally found on coastal sage leaves (Harrison et al. 1971) can act as protective SO_2 filters during field fumigations will depend upon exposure conditions.

Lower SO_2 concentrations exited the cuvette then entered the cuvette. For example, in the 0.1 ppm experiment with Q. kelloggii SO_2 concentrations leaving the cuvette ranged from 0.03 ppm to 0.07 ppm. SO_2 concentrations leaving the cuvette varied between 0.09 ppm and 0.14 ppm for the 0.2 ppm treatments and between 0.30 ppm to 0.42 ppm for the 0.5 ppm treatments. SO_2 flux rates were calculated at regular intervals for each experiment and were integrated over the 8 h fumigation to calculate the total quantity of SO_2 that each leaf absorbed. In order to compare experiments within the 0.1 ppm, 0.2 ppm, and 0.5 ppm treatments, the quantity of total SO_2 absorbed in each experiment was normalized to 0.06 ppm, 0.12 ppm, and 0.36 ppm, respectively. For example, in the experiment with Q. kelloggii described above the SO_2 concentration of 0.03 ppm was used to calculate SO_2 flux rates, which in turn were used to calculate the quantity of SO_2 absorption during

the experiment. The calculated absorption value was multiplied by two to represent an estimated absorption value for a hypothetical fumigation at 0.06 ppm. The example of Q. kelloggii represents the most extreme correction; all other measured SO_2 concentrations leaving the cuvette were within 30% of the normalized concentration.

Normalized SO_2 absorption values for each plant were plotted in relation to their stomatal conductance values for water vapor in SO_2 -free air (Fig. 4). The linear relationship between control conductance values and normalized SO_2 absorption values reflects the importance of conductance to SO_2 absorption into leaf tissues. The equations for lines in Figure 4 suggest that total SO_2 absorption can be predicted for some mediterranean-type plants when SO_2 concentrations around the plants are 0.06 ppm, 0.12 ppm, or 0.36 ppm.

SO_2 absorption can also be predicted in relation to conductance for any SO_2 concentration between 0 and 0.36 ppm. Increasing SO_2 concentrations around the leaves from 0.06 ppm to 0.12 ppm and to 0.36 ppm resulted in progressive changes in the slopes and Y intercepts of the lines in Figure 4. The slopes and Y intercepts of these regression lines were plotted in relation to increasing SO_2 fumigation concentrations (Fig. 5), and were found to change linearly with SO_2 concentrations. Thus, the curves in Figure 5 can be used to interpolate the slopes and Y intercepts which represent linear equations for total SO_2 absorption following 8 h fumigations at any concentration less than 0.36 ppm. For example, control stomatal conductance and SO_2 absorption during a 0.15 ppm fumigation are related by the straight line equation: $Y = -4.3 + 4.6X$.

Predicting the SO_2 absorption, at specific SO_2 concentrations, on the basis of leaf conductance values, may be a useful first step in screening species for relative SO_2 resistance in the field. Many techniques are currently available for

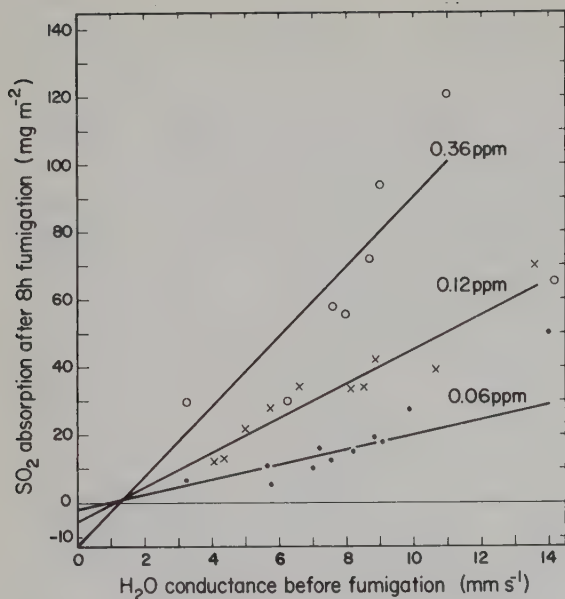


FIGURE 4. Leaf absorption of SO_2 during 8-hour fumigations are plotted against conductance values determined at the beginning of the experiment in SO_2 -free air. The SO_2 absorption values for fumigations at 0.1 ppm, 0.2 ppm, and 0.5 ppm are normalized to represent concentrations of 0.06 ppm (\cdot), 0.12 ppm (\times), and 0.36 ppm (\circ), respectively. Regression equations are as follows: 0.06 ppm = $Y = 1.03 + 2.04X$ ($r^2 = .83$); 0.12 ppm = $Y = -3.76 + 4.75X$ ($r^2 = .91$); 0.36 ppm = $Y = -10.1 + 10.2X$ ($r^2 = .85$). See text for further explanation.

accurately measuring stomatal conductance. In addition, no elaborate fumigation systems would be required for this screening technique.

The link between predicting relative SO_2 resistance between species on the basis of control conductance values lies in understanding the relationships between SO_2 absorption and photosynthetic decline. SO_2 can depress photosynthesis 1) by altering conductance and 2) by the phytotoxic effect on nonstomatal components of photosynthetic processes. These two factors may work in different combinations for two species and may explain why *D. aurantiacus* and *H. arbutifolia* did not have identical patterns of photosynthetic change in response to increased quantities of SO_2 absorption (Fig. 6).

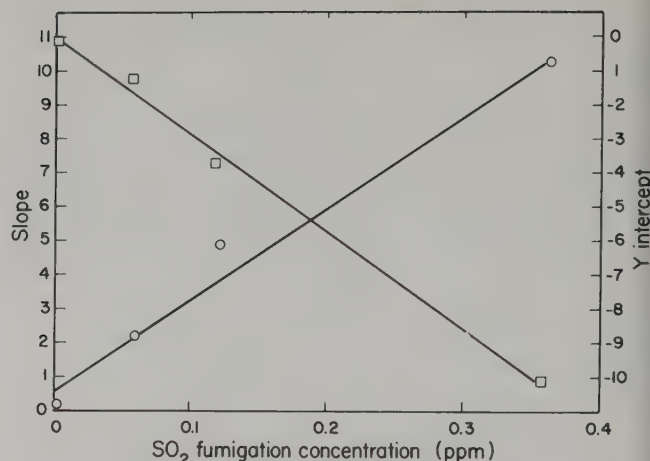


FIGURE 5. The slopes (\circ) and Y intercepts (\square) of regression equations from Fig. 4 plotted in relation to SO_2 fumigation concentrations. Regression equations are as follows: Y intercept = $Y = -0.143 + 28.6X$ ($r^2 = .99$); slope = $Y = 0.505 + 27.7X$ ($r^2 = .98$).

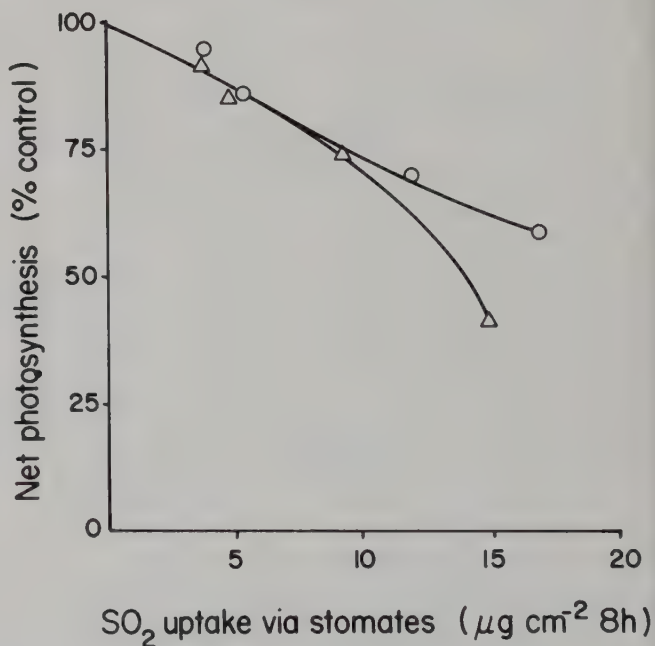


FIGURE 6. Relative change in photosynthesis for *D. aurantiacus* (Δ) and *H. arbutifolia* (\circ) following fumigation as a function of SO_2 absorption. Figure is modified from Winner, Mooney (1980b).

Figure 7 clarifies the effect of increasing SO_2 absorption on relative photosynthetic rates of these two species. Stomatal factors seem to play a larger role in inhibiting photosynthesis of *H. arbutifolia*. On the other hand, the non-stomatal components of photosynthesis for *D. aurantiacus* seem the more sensitive to SO_2 absorption.

Even though the photosynthetic response to SO_2 absorption is complex, the trend is clear; SO_2 absorption capacity is positively correlated with control conductance, and greater quantities of SO_2 absorption result in greater relative depressions of photosynthesis. Evaluation of the range of photosynthetic resistance to SO_2 absorption, particularly between species with a wide range of SO_2 resistances, may be a promising area for future studies.

4.4. Stomatal responses to the environmental milieu

The capacity to predict photosynthetic responses of plants and ultimately to forecast relative SO_2 resistances of many species may hinge upon knowing the conductance values of plants when they are fumigated. The dashed and solid curves of Figures 8A-H represent the range of generalized conductance responses to environmental and time gradients which are thought to occur for mediterranean-type shrubs. Dashed curves generally represent evergreen plants, solid curves represent deciduous sage plants. For example, curves in solid lines in Figures 8A and B depict the temporary nature of drought-deciduous leaves, whereas the dashed curves show generalized trends of conductance with time and age for evergreen leaves. The remaining curves are generalized from the theory that deciduous sage species have fewer mechanisms for conserving water and that evergreen species have optimal conductances only during times when water supplies are non-limiting (Mooney, Dunn 1970). Therefore, the

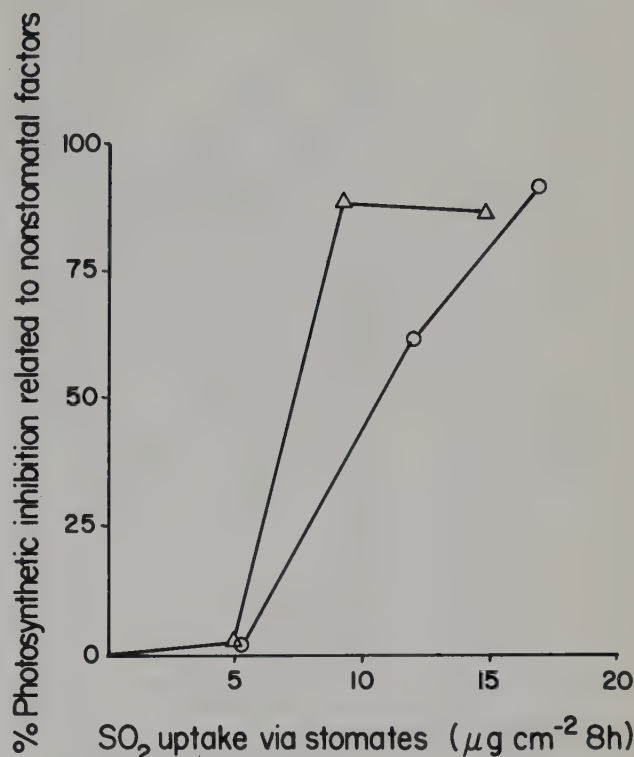


FIGURE 7. The percentage of total photosynthetic inhibition attributed to nonstomatal factors following 8-hour fumigations plotted against SO_2 absorption for *D. aurantiacus* (Δ) and *H. arbutifolia* (\circ). Figure is modified from Winner, Mooney (1980b).

dashed curves in Figures C-H suggest that evergreen species decrease their conductance at the first signs of heat, water, or SO_2 stress. On the other hand, solid curves in Figures C-H suggest that deciduous sage plants have high conductances over a broad range of environmental conditions.

Surveys of conductance values for mediterranean-type plants may verify the generalized scheme of water conservation represented above. Such a survey may be useful for projecting time periods when leaf conductances will be high and plants therefore are likely to absorb large quantities of SO_2 . These curves may also indicate the times when deciduous sage plants are likely to have higher conductances and therefore be prone to higher SO_2

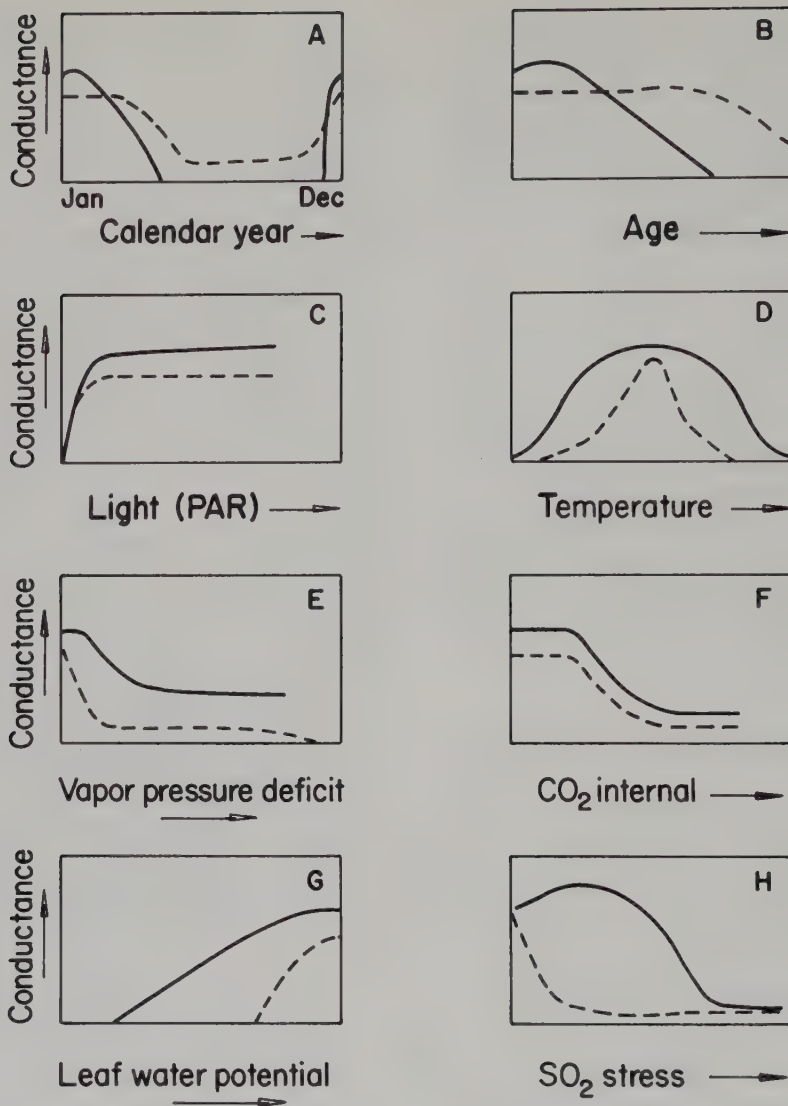


FIGURE 8. Generalized conductance response patterns of mediterranean-climate shrubs to an array of environmental and time gradients. Solid and dashed curves represent the relative ranges of shrub responses. See text for further discussion.

absorption rates than evergreen plants. Thus a basic survey of conductance values would not only contribute to our understanding of plant-water relations in water-stressed habitats but also contribute towards developing the capacity to predict SO₂ responses of plants in the mediterranean-type climate.

5. SUMMARY

Five evergreen chaparral species and five deciduous species were surveyed for several leaf characteristics and for the effects of SO₂ on photosynthesis and transpiration. The deciduous species generally had higher photosynthesis rates on an area, dry weight, and N basis as well as higher stomatal conductance

values. SO_2 caused temporary increases in photosynthesis and conductance in some experiments, but metabolic values at the end of 8 hours were lower than control values. Total SO_2 absorption into mesophyll tissues was linearly related to control conductance values. Thus, conductance values in SO_2 -free air may be an indication of the capacity of a plant to absorb SO_2 .

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1. INTRODUCTION

The ecophysiological characterization of the net assimilation of CO₂ is an important approach to the optimization of all forms of productivity in grapevine (primary production and crop yield) and quality. It must also be taken into account that the criteria for defining photosynthetic efficiency depends on the particular environment under analysis and that external conditions highly favorable for photosynthesis do not necessarily increase fruit production (Kriedemann, 1977).

Some basic physiological data on these topics have already been obtained in Australia (Kriedemann *et al* 1968, 1971 and Smart, 1974), California (Kliever *et al* 1970) and USSR (Stoev *et al* 1966).

More recently Carboneau *et al* (1978, 1979) have used bioclimatic and physiological information of grapevine in agronomic experiments. New training systems which conciliate wine quality and yield have been successfully tried in the Bordeaux region.

In Southern countries like Portugal vineyards are normally exposed to extreme environmental factors such as high solar radiation, high air temperature and water shortage. All these parameters will interfere with the ratio acid/sugar, the aroma, the coloring intensity and the yield.

The present paper deals with the study of some physiological aspects of grapevine photosynthesis particularly the response to high temperatures, different light intensities during growth and water stress.

Screening for specific cultivar behavior may also be an effective way of future manipulation in areas of quality or ecological adaptation.

The experiments were realized in three cultivars and the effects of leaf age and time of the day were also followed.

2. MATERIAL AND METHODS

2.1. Plant material

The *Vitis vinifera* cultivars studied were João Santarém, Tinta Amarela (wine grape varieties) and Rosaky (table grape variety). João Santarém is widely distributed in Central Portugal and Tinta Amarela in the Douro region.

Plants were grown either in pots in the glasshouse (about 70% of full sunlight) or outdoors in one cubic meter containers under plastic shading cages (experiments at 100%, 70% and 40% full sunlight) or in the field.

2.2. Laboratory measurements

A standard Warburg technique (Umbreit *et al*, 1974) was used for measuring net photosynthetic and dark respiration rates. The illumination for photosynthetic experiments was 200 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$ Ph AR, unless otherwise stated (also 100 and 55 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$ in section 3.3). The buffer 0,1 M Na₂CO₃/NaHCO₃ was employed.

Chlorophyll was measured according to the method of Arnon (1949). Sugars (reducing and soluble, after invertase hydrolysis) were determined by the Sumner's method (1925) and anthocyanins following Ribéreau-Gayon methodology (1971).

2.3. Field observations

Gross photosynthesis was determined using a ¹⁴C ventilated diffusion porometer (Model VP 1C, Cayuga development) designed according to Bravdo (1972). The assimilation time was 30 s and the radioactivity incorporated by the tissue was measured by liquid scintillation.

Stomatal resistance was estimated with the same diffusion porometer and leaf water potential with a pressure bomb (Sholander *et al*, 1965).

Photosynthetic active radiation (Ph AR) was determined using a quantum meter from Lambda (Model LI-170).

3. RESULTS

3.1. Photosynthesis in relation to temperature.

Influence of light conditions during growth, leaf age and cultivars.

The photosynthetic response to temperatures from 26° C up to 50° C is presented in fig.1 (results from July 1979).

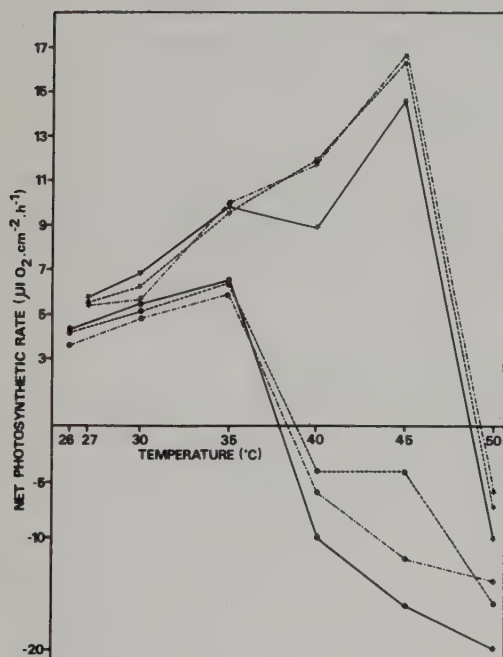


FIGURE 1. Leaf net photosynthesis of Tinta Amarela (★) and Rosaky (●) vines grown under 100% (—) 70% (---) and 40% (---) full sunlight as a function of temperature. Mean values from July 1979.

Cultivar Tinta Amarela and Rosaky grown under 100 %, 70% and 40% full sunlight show dissimilar responses particularly from 35° C up.

In both cultivars there is a steady rise until 35° C but in Tinta Amarela the sudden decrease is at 50° C while in Rosaky it is at 40° C.

The influence of light conditions during growth is not great. However 100% full sunlight grown plants seem more sensitive to higher temperatures than the shade grown ones. The experiment was repeated in 1980 (fig.2) with one more variety

(João Santarém) and using Rosaky leaves of three ages (terminal, mature and basal leaves).

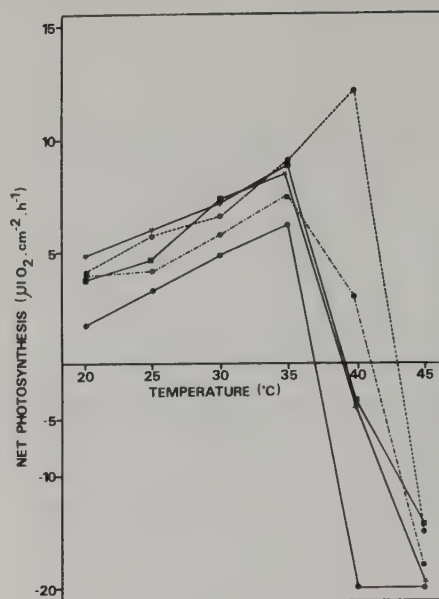


FIGURE 2. Leaf net photosynthesis of the cultivars Tinta Amarela (---), João Santarém (---) and Rosaky (—) (terminal ●, mature ★ and basal ■ leaves) as a function of temperature. Mean values from May 1980.

It was found again that Tinta Amarela had a better performance than the other two cultivars at temperatures over 35° C. This time however net photosynthesis fell to zero near 45° C. João Santarém presented an intermediate pattern - photosynthetic rate declined by 40° C.

Comparing the responses of leaf ages it can be seen that terminal leaves have lower photosynthesis at all temperatures and a sharper decrease at 40° C. Dark respiration rates were also measured (fig.3) at increasing temperatures and again cultivars showed a different behavior. In Tinta Amarela respiration continuously increased with temperature. In contrast Rosaky respiration become sensitive to temperature at 45° C.

Decreasing irradiance during growth seems to have a lowering effect on respiratory rates in both varieties.

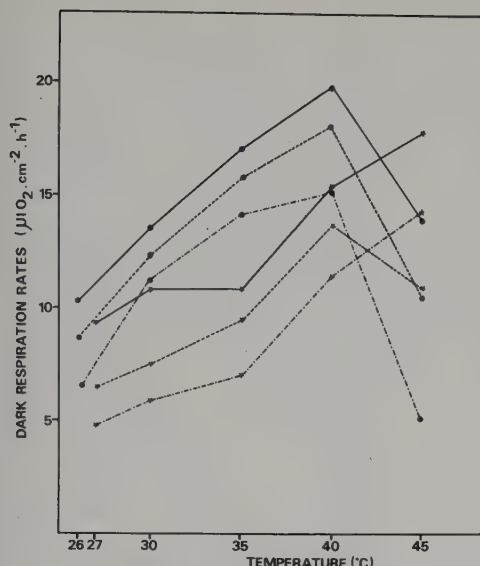


FIGURE 3. Dark respiration rates of Tinta Amarela (★) and Rosaky (●) grapevines grown under 100% (—), 70% (---) and 40% (····) full sunlight in relation to temperature. Mean values from July 1979

3.2. SLW, soluble and reducing sugars in different cultivars and leaves of three ages.

The characterization of the cultivars under study, including the effect of leaf age, was made in respect to leaf specific weight (SLW), leaf sugars (reducing and soluble), chlorophylls (a, b and a/b ratio) and leaf anthocyanins (table 1). All values are means from measurements made throughout the vegetation period, except for anthocyanins which appear at significant levels only at the end of vegetation.

SLW was normally higher in mature and basal leaves than in terminal leaves. No consistent differences between cultivars were found in this parameter. The same is valid for sugars and chlorophyll.

Carbohydrates showed a large variability due to seasonal fluctuations. Younger leaves generally had reduced levels of sugars and total chlorophyll which is in agreement with their lower net photosynthetic rates (fig.2). On the contrary chlorophyll a/b ratios were higher in the immature leaves.

Leaf anthocyanins contents were considerably higher in T. Amarela than those found in J. Santarém or Rosaky cultivars and seem to be well correlated with the coloring intensity of the berry skin.

3.3. Photosynthesis in relation to temperature and illumination (laboratory measurements). Influence of leaf age and cultivars.

The effects of low light intensities (200, 100 and 55 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$) on photosynthesis at three different temperatures (25°C, 30°C and 35°C) were measured on the cultivars T. Amarela, J. Santarém and Rosaky (fig.4 and table 2) under laboratory conditions. Leaves from inside the vine canopy frequently receive irradiances which are near to the light compensation point.

No-significant differences among cultivars were expected for 200 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$ in this range of temperatures according to previous results (fig.1 and 2).

A general decline of net photosynthesis with decreasing light intensities was observed in all cultivars and temperatures.

The data obtained at 55 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$ and expressed in percentage of the 200 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$ values, for the corresponding temperatures, are shown in table 2.

TABLE 2. Percentage reduction in photosynthesis of 55 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$ as compared to that at 200 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$.

		25°C	30°C	35°C
T. Amarela		63%	28%	24%
J. Santarém		49%	42%	52%
	apical	68%	-17%	-96%
Rosaky	mature	46%	21%	23%
	basal	52%	22%	25%

Higher temperatures seem then to stress the negative effect of the low light intensity. In addition younger leaves (fig.4A) are particularly affected by this combination of low light and high temperature.

TABLE 1 - Specific leaf weight, reducing and soluble sugars, chlorophyll and anthocyanin contents from leaves (terminal, mature and basal) of the cultivars *Tinta Amarela*, *João Santarém* and *Rosaky*. Each estimate is the mean value affected by the standard deviation.

<i>Tinta Amarela</i>				<i>João Santarém</i>				<i>Rosaky</i>			
Type of leaves	Terminal	Mature	Basal	Terminal	Mature	Basal	Terminal	Mature	Basal	Terminal	Basal
SLW g. dm ⁻²	FW	16.6±1.1	19.4±0.6	20.1±0.9	16.9±2.3	19.4±0.3	19.0±0.4	17.1±1.4	20.1±2.1	20.9±1.5	
	DW	3.0±1.4	5.0±0.9	4.2±1.0	3.4±0.1	5.6±0.6	4.9±0.1	4.5±0.9	5.2±0.9	5.4±1.2	
Sugars mg. g ⁻¹ .w.	Reducing	30.5±12.0	36.5±10.0	43.6±12.3	28.0±8.3	33.8±11.5	30.0±6.9	33.7±6.5	33.8±12.0	32.6±10.4	
	Soluble	40.4±12.0	52.0±15.1	56.7±7.5	43.2±13.5	53.9±13.0	53.4±13.6	50.3±6.6	55.6±6.8	60.1±15.1	
Chlorophylls mg. dm ⁻²	a	1.2±0.3	1.8±0.3	1.6±0.2	1.3±0.1	2.0±0.4	1.9±0.3	1.3±0.1	1.9±0.2	1.8±0.2	
	b	0.3±0.1	0.4±0.1	0.5±0.04	0.4±0.1	0.6±0.1	0.5±0.1	0.3±0.02	0.5±0.03	0.5±0.04	
	total	1.5±0.4	2.2±0.3	2.0±0.2	1.7±0.4	2.6±0.6	2.4±0.2	1.6±0.2	2.4±0.3	2.5±0.2	
	a/b	4.9±0.7	4.1±0.6	3.2±0.7	4.0±1.2	3.4±0.4	3.7±0.4	4.1±0.7	4.1±0.2	3.5±0.1	
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Anthocyanin mg. g ⁻¹ .w.		—	42.0	—	—	16.8	—	—	7.5	—	—

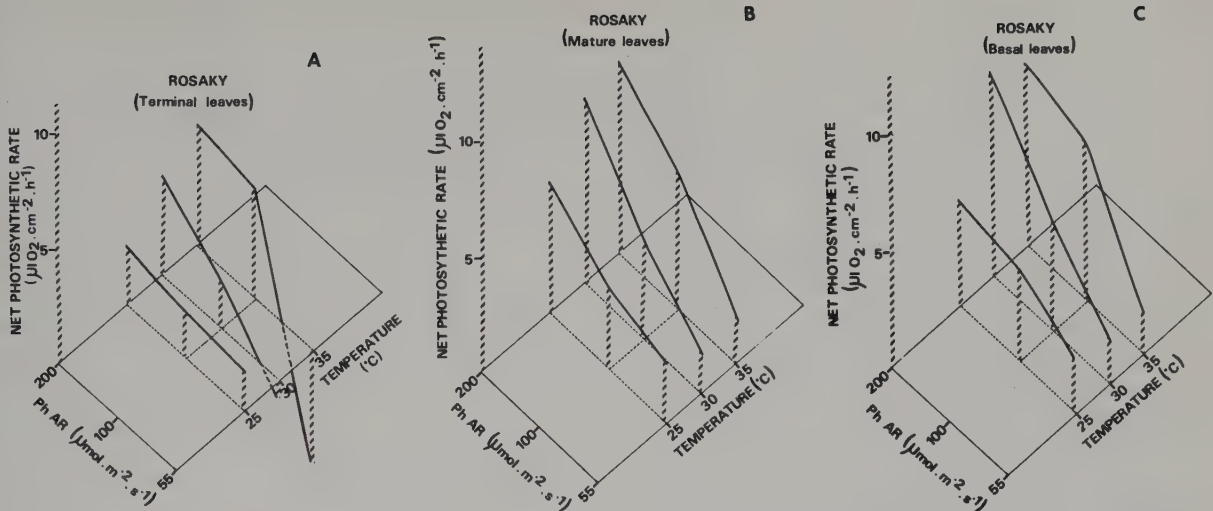


FIGURE 4. Response of vine leaf photosynthesis, cultivar Rosaky, to photosynthetic active radiation (Ph AR) and temperature in laboratory conditions. A - Terminal leaves; B - Mature leaves; C - Basal leaves.

In fact, for these leaves and 25°C , the light compensation point was not yet reached at $55\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. At 30°C and 35°C at the lowest light levels there was no net photosynthesis. For mature leaves of these cultivars light compensation points are still below $55\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

At $100\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ the percentage reduction from $200\text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ values found in photosynthetic rates ranged, according to temperature, from 63% to 88% in T. Amarela, 68% to 97% in J. Santarém and 53% to 72% in Rosaky, for mature leaves. The results with young leaves were 51% to 96% and with basal leaves were 52% to 98%. At this intermediate irradiance, however, higher temperatures did not always correspond to the highest depression on photosynthesis.

3.4. Water availability effect on photosynthetic rate.

The response of net photosynthesis to decreasing water potentials is shown in fig.5 for Rosaky vines grown in one cubic meter containers.

Two experimental procedures were followed. In the first one terminal, mature and basal leaves from plants subjected to water stress over a five week

period were analyzed for net photosynthesis and water potential. Photosynthesis showed signs of decrease at leaf water potentials below -7 bars but a sharp decline (about 80%) was obtained only at about -14 bars. A similar behavior was apparent for the different leaf ages.

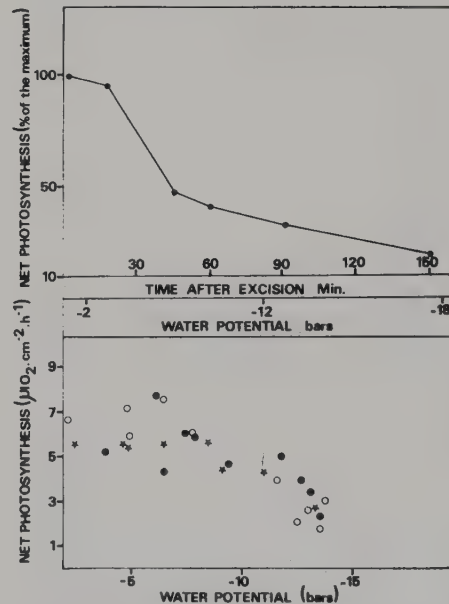


FIGURE 5. Photosynthetic response to leaf water potential. Above: leaf excision experiment for the Rosaky cultivar. Below: Rosaky leaves of three ages subjected to slow water stress (terminal ●, mature ○ and basal ★ leaves).

The second experiment (fig.5 above) involved an excision of the leaf (fully turgid at zero time) and the consequent water stress induced by it. For a period of 20 minutes there after the net photosynthetic rate remained fairly constant, dropping then to approximately 50% of the original value for ψ near -7 bar.

Water potentials of -18 bar were in this case obtained with a parallel 90% reduction of the photosynthetic rate. In spite of a drastic change in ψ and P_N values in a much shorter period of time in the excision method the pattern of the two experiments was quite comparable.

3.5. Diurnal trends in photosynthesis, leaf sugars and stomatal resistances.

Diurnal patterns of leaf gross photosynthesis as well as leaf diffusive resistance (r_s) were followed in Rosaky plants grown either in the vineyard or in the greenhouse (fig.6). Irradiance and air temperature were also recorded.

The data collected show an increase, both in field or greenhouse vines, of gross photosynthesis up to midafternoon and a subsequent decline at 18.00h. Significant differences were found between vineyard and shade house plants for that parameter at the beginning or at the end of the day, which is logical due to the lower irradiances at that time.

In both cases there was not any midday depression which has been often reported in some crops (Sawada, 1978).

Diurnal patterns of sugars followed rather closely solar radiation and air temperature curves (fig.7) in a manner like photosynthesis.

Stomatal resistance remains almost constant up to 15.00h presenting some rise only by late afternoon. This is consistent in terms of the r_s light response (fig.8) owing to the fact that closing of stomata started for photosynthetic Active Radiation between 100 and 200 $\mu\text{moles.m}^{-2}.\text{s}^{-1}$. On the same figure one can observe that for identi-

cal Ph AR the stomatal resistances of grapevines grown under field conditions are normally lower than the r_s of greenhouse plants. This feature could possibly be explained from the lower stomatal densities found in shade grown vines (Chaves, 1980).

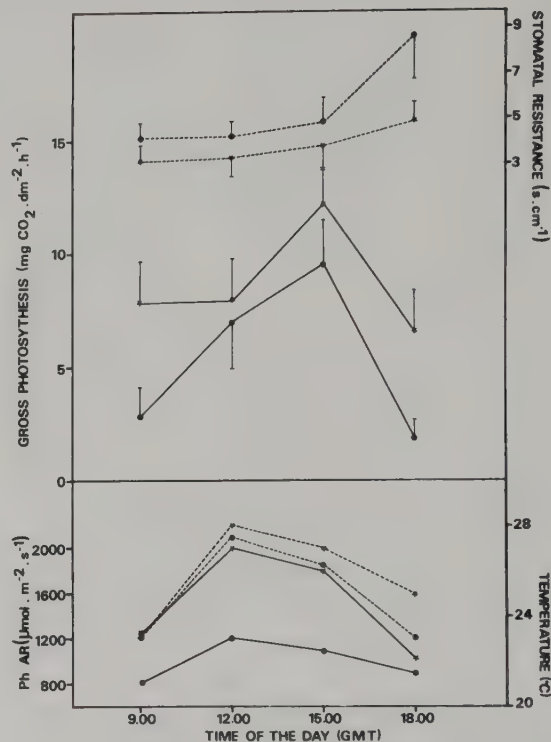


FIGURE 6. Diurnal course of leaf gross photosynthesis (GP), leaf diffusion resistance (r_s), air temperature (---) and photosynthetic active radiation (—). Mature leaves of Rosaky grapevines grown under field (★) or greenhouse (●) conditions. Vertical bars represent mean confidence intervals at 5% level.

In addition to leaf diffusion resistance internal resistance was also calculated, according to Gaasstra (1959), during the entire day and for field and greenhouse plants (fig.9). A perfect negative correlation was established between gross photosynthesis and internal resistance. The values for internal resistance, which include the CO_2 diffusion resistance in the mesophyll and carboxylase resistance, were of an order of magnitude much larger than r_s . In fact in this non-water stress conditions internal resistance may possibly be the main

resistance factor responsible for gross photosynthetic variation.

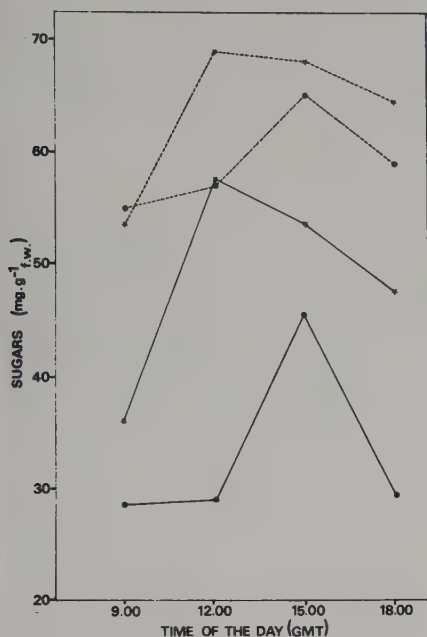


FIGURE 7. Diurnal changes in reducing and soluble sugars of Rosaky leaves from shade house (●) or field grown plants (★).

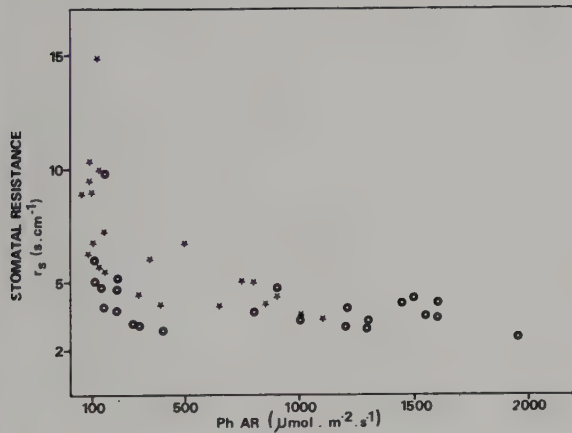


FIGURE 8. Stomatal diffusive resistance as a function of Photosynthetic Active Radiation (Ph AR). Rosaky leaves (field ● and shade house ★).

4. DISCUSSION

Photosynthetic response to temperature was clearly positive for all cultivars until 35°C. Nevertheless one cultivar (T.Amarela) which curiously comes from one of the Portuguese hotter re-

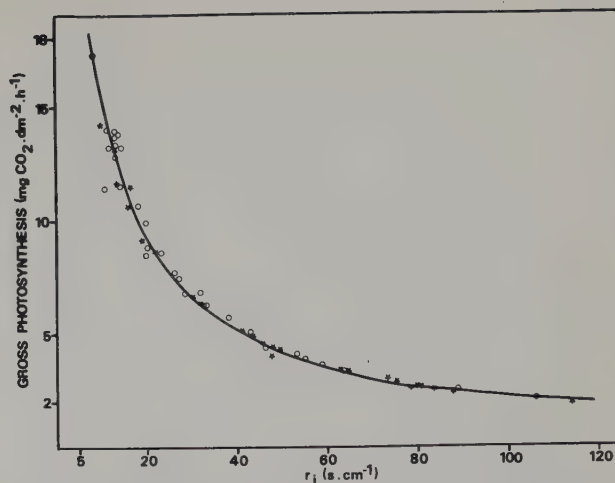


FIGURE 9. Gross photosynthesis/internal resistance relationship from Rosaky leaves (field ○ and shade house ★).

gions, presented still a greater response at 40°C or even 45°C. These temperatures are somewhat higher than the optimum of 30°C indicated by Kriedemann (1971) under Australian conditions. It can in part be explained by the experimental conditions (humidity saturated atmosphere) which were not favourable to desiccation of the tissues, probably the chief reason (Kriedemann, 1977) for the negative effects on photosynthesis caused by high temperature.

It seems apparent from the results presented some kind of cultivar adaptation to temperature either due to a better resistance to tissue desiccation or to a thermal stability of Calvin cycle enzymes.

In addition an increase in temperature (for example from 25°C to 35°C) can raise light compensation points, an effect predominantly adverse for leaves inside a dense canopy.

The temperature dependence of the light compensation point, explained by differential effects on the rates of photosynthesis and respiration, was especially pronounced in younger leaves.

The physiological characterization of immature leaves is of importance in grapevines since in some varieties the presence of lateral shoots contribute to a significant percentage of foliar sur-

face.

In the present experiments the light compensation point for younger leaves came at Ph AR values at about $75 \mu\text{moles.m}^{-2}.\text{s}^{-1}$ at 35°C or $65 \mu\text{moles.m}^{-2}.\text{s}^{-1}$ at 30°C , while the generally cited values (Kriedemann, 1977) are around $20 \mu\text{moles.m}^{-2}.\text{s}^{-1}$. Other characteristics of immature leaves were lower photosynthetic rates at all temperatures, lower carbohydrate contents when compared with the mature leaves. Higher chlorophyll a/b ratio was also found.

The critical values of water potential found in these experiments with Rosaky grapevines subjected to a slow drying cycle were -7 to -8 bar for a slight decrease in net photosynthesis and around -13 bar for 80% reduction of that rate. No significant differences were found among leaf ages. In previous studies critical values of similar magnitude were found for other cultivars (Rodrigues and Chaves, 1979).

Some diurnal patterns of vine net photosynthesis have already been presented by Pogocian (1970) Kriedemann (1971) and more recently Lange and Meyer (1979). An apparent discrepancy arises from the comparative analysis of the different results.

The first author found a midday depression on photosynthetic rate from flowering till maturation and its disappearance thereafter. Lange also reported midday depressions in grapevine net CO_2 exchange restricted to the second part of the summer period which he links to an increased stomatal resistance induced mainly by low ambient air humidity.

In contrast with these data the results presented here show no midday depression in gross photosynthesis and no stomatal closing (experiments performed in July). This is in agreement with P_N pattern obtained by Kriedemann as well as by other authors for other plants (Sawada, 1979). It seems reasonable to conclude that photosynthetic diurnal trends, integrating the response

to numerous factors, may be greatly influenced by the previous ecophysiological history of the plant. Grapevine seems however to support in many conditions the midday stress with no stomatal closure and no photosynthetic depression which is of positive ecological significance, if in the presence of good water supply.

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CARBON ALLOCATION TO ROOT SYSTEMS IN MEDITERRANEAN EVERGREEN SCLEROPHYLLS

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1. INTRODUCTION

Although root:shoot biomass ratios provide some insight into carbon allocation to the main plant organs (about 50% of the biomass can be considered carbon), these data do not suffice to describe the annual pattern of carbon allocation to root systems. There are fundamentally three carbon sinks in the heterotrophic root system which have to be considered. The first one is the fraction of carbon used for growth in length and thickness. In a general way, the distribution of secondary thickening in root systems was analyzed by Wilson (1975). Yet, specific data are not available. Avila et al. (1978) estimated for Colliguaya odorifera, a Chilean sclerophyllous matorral shrub, that about 10% of the total yearly biomass increase is the result of secondary growth. A similar value resulted from analysis of Cryptocarya alba another evergreen sclerophyllous shrub in the same ecosystem (G. Avila, personal communication).

The second fraction of carbon used in root systems is needed for growth of the ephemeral rootlet population. Diameters of these rootlets in mediterranean-climate shrubs oscillate around 0.5 mm. We do not have much information concerning their longevity. According to our own observations of chaparral shrubs grown in containers with show-windows we are inclined to estimate that in general the mean rootlet is functional for 3-4 months. In a 25-year southern California mixed chaparral with Adenostoma fasciculatum, Ceanothus greggii, Arctostaphylos glauca, and Rhus ovata as the main shrub species, it was estimated that about 1000 g of rootlets, including some larger root tips, were produced per m² in a growing season (Kummerow et al., 1978).

Unknown is the amount of biomass lost by sloughing off of root cap cells and mucilage by root tips. That this amount might be substantial was suggested by Samtsevich (1965) who estimated that the total amount added to the soil in a wheat field was equivalent to the dry weight of grain harvested. Furthermore in our study rootlet estimates were based on soil core extractions. Large multiplication factors and the heterogeneity of the soil resulted in rather large error bars for the data. It had been suggested by Reynolds (1975) that rootlet populations in the soil under a closed canopy of a mature Douglas fir stand show activity in distinct soil cells of relatively small size (0.6 m). Thus, sample size of soil cores may be a decisive element in rootlet biomass estimates.

The third of the carbon fractions allocated to the root system is used for growth and maintenance respiration. It is obvious that with an increasing mass of living roots and rootlets this fraction must also increase.

The purpose of this study is to compare the rootlet biomass data obtained from chaparral soil cores with information gathered from container-grown chaparral shrubs where quantitative rootlet harvests were feasible. If rootlet biomass values from the container-grown shrubs support the rootlet biomass values from the chaparral, a substantially higher fraction of the fixed carbon is allocated to the root system than was conventionally estimated.

2. MATERIALS AND METHODS

Four shrubs each of Colliguaya odorifera Mol. and Quillaja saponaria Mol. native in the Chilean matorral and three Rhus ovata Wats. from the southern California chaparral were grown in red-

wood containers from the seedling stage to two years of age. These shrubs are typical representatives of the evergreen sclerophyllous shrub flora of the mediterranean-climate vegetation. At harvest time in January and February, 1980, these shrubs had grown to an average height of 1.5 m and their canopy covered a surface area of 0.2 to 0.4 m² (mean 0.3 m²). The box dimensions were 0.2 and 0.6 m in width and length respectively and 0.7 m in depth. The soil was a mixture of sand and peat moss and watering and fertilizing followed routine nursery practice with an automatically controlled drip irrigation system. The containers were installed in a courtyard of San Diego State University which resembles somewhat the conditions of a chaparral ravine with slightly reduced light intensity.

Dismantling of the growth containers showed that after two years the roots grew so as to rather homogeneously occupy the soil volume available. Eight cores of 125 cm³ were extracted randomly from each box after the dismantling of one of the side walls. The cores were analyzed for rootlets according to a previously described method (Kummerow et al., 1978). This technique consists basically of washing the soil samples through different sized sieves and hand sorting the rootlet mass into dead and live material. The results were used to calculate the total amount of dead and live rootlets per shrub. Roots with more than 1 mm diameter were collected by washing the entire box contents through a coarse sieve (mesh diameter 3 mm) which did not retain the thinner and fragile rootlets. In addition, leaf and stem dry weights were collected.

3. RESULTS

3.1. The above- and below-ground biomass. Biomass values of the eleven harvested shrubs, four Colliguaya odorifera, four Quillaja

saponaria, and three Rhus ovata shows some heterogeneity in spite of their identical age and growing conditions (Table 1). However, the root:shoot biomass ratios (r:s ratio) are relatively uniform, an indication perhaps of the needed balance between these two plant compartments. A special case presented Quillaja saponaria No. 2. The r:s ratio was twice as high as that of the other three shrubs of this species. This shrub had been damaged by a storm in summer, 1979 and, as a consequence, the stems had been trimmed off and discarded. The finally harvested biomass from aboveground was only three months old, consisting of vigorous stump sprouts with young foliage. The rootlets had also obviously suffered because only three grams (dry weight) could be harvested. The live rootlet:leaf biomass ratio in this shrub was 0.11 vs. a mean of 0.34 from the other three Q. saponaria plants. The corresponding ratio in C. odorifera was 0.44 (range 0.33-0.56) and in R. ovata were 0.50 (SD 0.07), 0.32 (SD 0.11), and 0.45 (SD 0.15) mm respectively. The leaves of these three shrub species have about the same density, i.e., 0.027 g cm⁻² (Fishbeck, Kummerow, 1977).

3.2. Relative contribution of plant organs to the total biomass.

In the three analyzed species between 7% and 11% of the standing live biomass was found as living and 2.5%-3.5% as dead rootlets. This latter value is somewhat arbitrary because it is difficult to distinguish between live and dead rootlets even with the use of a dissection microscope. In spite of the young age of the test plants 15%-23% of the total biomass was incorporated into the larger roots. Species differences may exist but our sample size was too small to consider these differences as significant (Fig. 1). The relative contribution of the foliage to the total biomass varied between species. In Colliguaya 20%, in Quillaja 27%, and in Rhus 35%

TABLE 1. Biomass distribution of rootlets, roots, leaves and stems in 11 2-yr evergreen sclerophyllous shrubs cultivated in redwood containers.

	Total biom. g	Rootlets live g < 1mm	Rootlets dead g < 1mm	Larger roots	Belowground biom. g	Leaves g	Stems g	Aboveground biom. g	r : s ratio
<u>C. odorifera</u>									
1	720	56	41	155	252	120	348	468	0.54
2	979	105	28	169	302	320	357	677	0.45
3	1220	167	30	269	466	298	456	754	0.62
4	1688	182	34	363	579	433	676	1109	0.52
<u>Q. saponaria</u>									
1	1432	107	28	199	333	339	760	1099	0.30
*2	318	3	27	142	172	28	118	146	0.85
3	2371	266	53	444	763	578	1030	1608	0.47
4	1847	153	60	221	434	632	781	1413	0.31
<u>R. ovata</u>									
1	1747	188	70	260	518	627	602	1229	0.42
2	1175	55	44	281	380	387	408	795	0.48
3	1389	70	7	300	377	524	488	1012	0.37

*Stump sprout

of the standing biomass were leaves. Stems contributed 35% (*Rhus*), 43% (*Colliguaya*) and 46% (*Quillaja*) to the total biomass. Overlapping of the values between species justified a mean value for the three evergreen sclerophyllous shrubs, cultivated under the described conditions: 12% rootlets, 19% larger roots, 28% leaves, and 41% stems described adequately the biomass distribution at harvest time (Table 2).

3.3. Comparison of 2-year container-grown shrubs with 25-year field-grown shrubs.

A comparison of young container-grown plants with mature shrubs harvested in early summer in the chaparral of southern California or the matorral of central Chile has to be evaluated with extreme caution. The leaf:stem biomass ratio of the container-grown shrubs ranged from 0.6 to 1.0 vs. 0.2 to 0.4 from mature, field-grown shrubs. This difference was expected because in mature chaparral shrubs a much higher proportion of the biomass will be found in the stems. It is also reasonable that the young, fertilized and irrigated plants have a

substantially higher leaf biomass per m² than the mature shrubs. The estimated LAI for *C. odorifera*, *Q. saponaria*, and *R. ovata* were 3.5, 4.0, and 4.5 respectively and thus substantially higher than the values for mature shrubs with 0.9, 1.7, and 1.9 in the same species order (Mooney et al., 1977).

According to our measurements of rootlet biomass in the chaparral, about 800 g m⁻² of living rootlets represent the average rootlet density under the canopy in the spring. This value increases to 1400 g m⁻² in summer and declines to 400 g m⁻² in winter (Kummerow et al., 1978). The difference between minimum and maximum, i.e., about 1000 g m⁻², is considered the annual rootlet production. The container-grown shrubs were harvested in winter and early spring. The mean live rootlet biomass for the 10 shrubs amounted to 451 g m⁻². Unfortunately, we do not have the seasonal minimum and maximum values. However, significantly less dead rootlets per m² were found. We speculate that the superior water and fertilizer conditions in the containers caused a faster rootlet turnover than in the field where soil moisture in July drops below

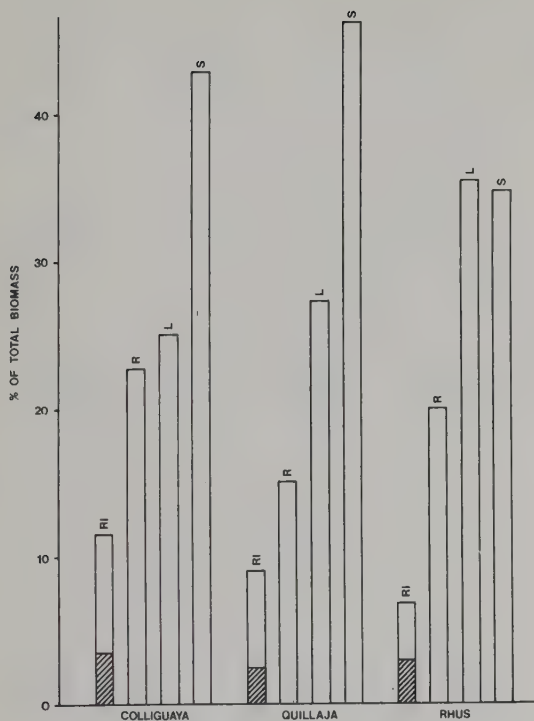


FIGURE 1. Biomass contribution in % of the total biomass of rootlets (RI, hatched part of column; dead, white part: live rootlets), roots with diam. > 1 mm (R), leaves (L), and stems (S) of three evergreen sclerophyllous shrub species. Each column is the mean of four (*Colliguaya*) and three (*Quillaja* and *Rhus*) individual shrubs. For range of values see Table 2.

0.1 g cm^{-3} of soil thus inhibiting growth of new rootlets and preventing decomposition of dead ones. The total annual rootlet production per m^2 in the container-grown plants appears to be similar to the one of chaparral grown shrubs.

4. DISCUSSION

The standing biomass of the major roots (diam. > 2.5 mm) of a typical 25-year mixed chaparral was estimated as 565 g m^{-2} (Kummerow et al., 1977). These major roots increase in diameter with the growth of the vascular cambium. It was estimated that these roots add about 10%

of their biomass per year (Avila et al., 1978). Thus, $56 \text{ g m}^{-2} \text{ yr}^{-1}$ is allocated to the secondary root growth in our chaparral site.

Of special significance is the question of rootlet production. We have stated above that $1000 \text{ g m}^{-2} \text{ yr}^{-1}$ for a mature chaparral stand is a reasonable estimate of fine root production. Unpublished results by G. Avila and S. Araya from the central Chilean matorral show that $1500 \text{ g m}^{-2} \text{ yr}^{-1}$ might be expected. Similar values have been shown for the Greek phrygana. On a 30 cm deep soil a seasonal root biomass fluctuation of 500 g m^{-2} was found. Since the larger roots are perennial this 500 g value must be mainly due to rootlet turnover (Margaris, 1976). Considering that these data were obtained on a soil base only half as deep as the chaparral soil, the two fine root biomass values are similar. In a mature central Swedish scots pine forest 300 g m^{-2} of fine roots were recorded and it was estimated that twice this value would correspond to the annual rootlet production (Persson, 1979). Thus, the values found in the chaparral do not seem to be unreasonable.

Rootlet biomass recovered from the container-grown shrubs vary according to the size of the harvested shrubs (Table 1). However, the relative rootlet densities as a percentage of the total biomass are more uniform and the calculated value of 9% live fine roots as a mean for the ten harvested shrubs appears to be representative (Table 2). The average shrub has a biomass of 1456 g dry weight. Thus, the mean fine root mass per shrub amounts to 135 g . The average ground cover of the harvested shrub was 0.3 m^2 . This translates the 135 g per shrub to 450 g m^{-2} . The small fraction of dead rootlets in the containers is surprising, reaching only an average of 133 g m^{-2} . The data from field core extractions indicated that at any time during the season at least the same amount of dead and live rootlets was present in the soil. We speculate that in the regularly watered and fertilized containers the normal lifespan of a rootlet is

TABLE 2. Relative biomass distribution in 10 evergreen sclerophyllous shrubs cultivated in redwood containers.

	Total biom. g	Rootlets live %	Rootlets dead %	Larger roots %	Leaves %	Stems %
<u>C. odorifera</u>						
1	720	8	6	22	17	48
2	979	11	3	17	33	36
3	1220	14	2	22	24	37
4	1688	11	2	21	26	40
\bar{x}		11	3	21	25	40
<u>Q. saponaria</u>						
1	1432	7	2	14	24	53
3	2371	11	2	19	24	43
4	1847	8	3	12	34	42
\bar{x}		9	2	15	28	46
<u>R. ovata</u>						
1	1747	11	4	15	36	34
2	1175	5	4	24	33	35
3	1389	5	1	21	38	35
\bar{x}		7	3	20	35	35
Mean 10 shrubs		9	3	19	29	40

shorter than in the field. Assuming that rootlets last about four months, the total rootlet production in the containers might be as high as $1350 \text{ g m}^{-2} \text{ yr}^{-1}$. As speculative as some of these calculations appear, there remains the observation that overall fine root biomass from field and container-grown shrubs fall into the same order of magnitude.

However, there is still some doubt regarding these conclusions. Oechel and Lawrence (1980) by using the ^{14}C dilution technique after Caldwell and Camp (1974) in the same research area, obtained a fine root turnover rate of $0.76 \text{ g g}^{-1} \text{ yr}^{-1}$. This value would require that about 24% of the rootlets stay alive for one year, and the annual fine root production might be smaller than the one found by us with direct soil extractions at monthly intervals. More investigations are required to clear this discrepancy.

An important fraction of the carbon assimilated by the foliage is required for growth and main-

tenance respiration of the root system. Recent studies by Oechel and Lawrence (1980) shed some light on this complex problem. Respiration for the root system of C. odorifera shrubs required 23% of the total annual biomass production. The corresponding value for R. ovata (29%) was even higher. Data for Q. saponaria are not available.

Our results on rootlet biomass production imply that the belowground litter production is substantially higher than the aboveground litter fall. Similar conclusions were reached for a 15- to 20-year pine forest in central Sweden (Persson, 1978) and a mixed deciduous forest in the eastern USA (Edwards and Harris, 1977). For the southern California chaparral mean annual litter production for 1972 and 1973 of eight major shrub species was estimated as 242 and 355 g m^{-2} respectively (Mooney et al. 1977). Since few soil organisms are transporting leaf litter into the chaparral ground and intensive winter rains wash litter from slopes into deeper ravines, the belowground litter production

of chaparral acquires special significance for soil formation.

5. CONCLUSIONS

Rootlet biomass production in the chaparral reaches $1000 \text{ g m}^{-2} \text{ yr}^{-1}$. Data from container-grown chaparral shrubs support this finding which implies that at least 12% of the annual carbon gain is allocated to rootlet growth. The belowground litter production is substantially higher than aboveground litter fall.

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CHANGES OF STORAGE LIPIDS, FATTY ACIDS AND CARBOHYDRATES IN VEGETATIVE PARTS OF MEDITERRANEAN EVERGREEN SCLEROPHYLLS DURING ONE YEAR

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1. INTRODUCTION

Information about the physiological behaviour of storage carbohydrates and lipids in plants of the mediterranean area is generally not available, or comes from older studies (Guttenberg 1927, Guttenberg, Buhr 1935 and Iljin 1929). On the contrary the seasonal variations of storage carbohydrates have been extensively studied in plants of central Europe (Jeremias 1964, 1969 and Diamantoglou 1974).

Therefore we studied the physiological behaviour of the storage carbohydrates and lipids in typical mediterranean-climate evergreen sclerophyllous plants; *Ceratonia siliqua*, *Quercus coccifera* and *Pistacia lentiscus*. The free sugar, starch and total lipid content in the bark and the leaves were investigated during one year. The fatty acid composition of the saponifiable lipids was determined by gas liquid chromatography. The cellular osmotic pressure of the leaves was also determined. Glucose, sucrose and small quantities of fructose were measured as free sugars.

2. PROCEDURE

2.1. Material and methods

2.1.1. Material. Leaves and bark of *Ceratonia siliqua*, *Quercus coccifera* and *Pistacia lentiscus* were examined. The sample material was collected during one year, in the middle of every month, at the same hour of the day (about 10 a.m.) to avoid daily variations. Leaves (completely developed) and peeled bark were boiled for 10 minutes in plastic bags and then were dried in an oven, equipped with a ventilator, at 60°C.

2.1.2. Methods. The total lipids were extracted from the dried material with a solution to chloroform-methanol (2:1 v) according of the method

given by Winter (1963). The total lipid content was determined from the extract. The methylesters of the fatty acids were produced by saponification of the lipids, according to Stoffel et al. (1959) and Bayer (1962). This process was accomplished under streaming nitrogen.

Gas chromatography: A Perkin-Elmer F 11, equipped with a flame ionization detector was utilized. The S.Steel column had a length of 6 ft., a diameter of 1/4 in. and contained 20% Diethylene glycol succinate on HMDS chromosorb W 80-100 mesh. The column temperature was 180°C and the injector temperature 210°C. N₂ was the carrier gas with a flow rate of 30 ml/min. The single peaks were determined according to Kull, Jeremias (1972). The quantitative determination of the fatty acids was done with the process given by Kaiser (1965) and Kull, Jeremias (1972). The amounts were given as % of the total fatty acid amount. The methylester of the pentadecanoic acid was used as internal standard.

The cellular osmotic pressure (Π*) was determined by the cryoscopic method using the cryoscope Drucker-Burian (Walter 1931, Thren 1934 and Walter, Kreeb 1970). The extraction of the sap for measuring the osmotic pressure was done according to Breckle (1966) and Breckle, Kull (1971). The extraction and quantitative determination of the sugars was done according to the method given by Jeremias (1958, 1965).

3. RESULTS

3.1. Total sugar content in the leaves and the bark of *Q.coccifera* (Figure 1)

In the leaves of *Q.coccifera* we observed a rise of the total sugar content during the hot and dry period in the summer that continued until October and then decreased. During the growth period in the

spring a new decrease of the total sugar content was observed.

In the bark of *Quercus coccifera*, as in the leaves, a rise of the total sugar content was observed during the dry period in the summer that reached the maximum in August and then decreased. The total sugars remained at the same level during the winter and the growth period. The total sugar content in the leaves was higher than in the bark, during the whole year.

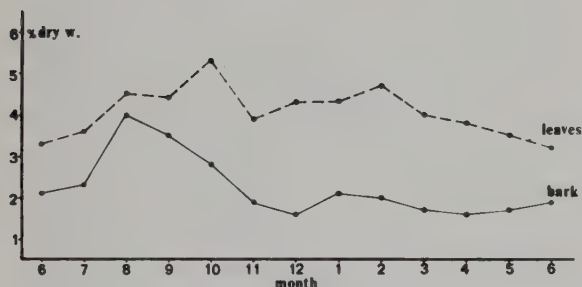


FIGURE 1. Content of total sugars in the leaves and the bark of *Quercus coccifera* during the course of a year (as % of dry weight).

3.2. Total sugar content in the leaves and the bark of *Pistacia lentiscus* (Figure 2).

As in *Quercus coccifera* the total sugar content in the leaves of *Pistacia lentiscus* increased during the summer, then a continuous decrease was observed until April. From May/June with the beginning of the dry period an increase of the total sugars was observed.

In the bark as in the leaves we observed a rise in the summer and a decrease in the winter, but before the beginning of the growth period the total sugar content increased and then decreased during the growth period.

3.3. Total sugar content in the leaves and the bark of *Ceratonia siliqua* (Figure 3).

In the leaves of *Ceratonia siliqua* the total sugar content changed differently than in *Quercus*

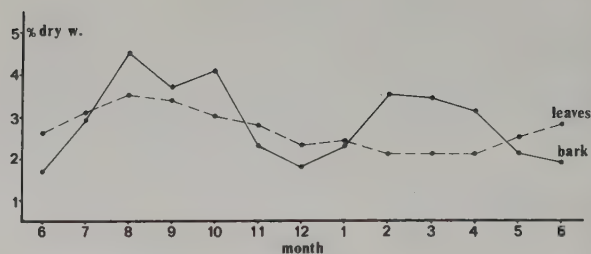


FIGURE 2. Content of total sugars in the leaves and the bark of *Pistacia lentiscus* during the course of a year (as % of dry weight).

coccifera and *Pistacia lentiscus*. During the summer in *Ceratonia siliqua* it was low and in the fall a slight rise was observed where it remained at the same level until February. With the beginning of the growth period the total sugar content increased considerably and from June with the beginning of the hot and dry summer period it decreased. In the leaves of *Ceratonia siliqua* the total sugar content was lower than in the bark during the whole year.

In the bark of *Ceratonia siliqua* we observed the same variations as in the bark of *Pistacia lentiscus*.

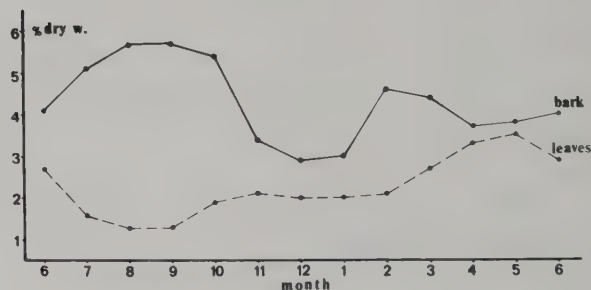


FIGURE 3. Content of total sugars in the leaves and the bark of *Ceratonia siliqua* during the course of a year (as % of dry weight).

3.4. Cellular osmotic pressure in the leaves of *Quercus coccifera*, *Pistacia lentiscus* and *Ceratonia siliqua*.

Figure 4 shows the variations of the cellular osmotic pressure (π^*) in the leaves of *Quercus coccifera*, *Pistacia lentiscus* and *Ceratonia siliqua* during one year and the changes in the amount of

the total sugars. With the increase of the total sugars during the summer we observed a parallel rise of the cellular osmotic pressure. No effect on carbohydrate storage and osmotic pressure could be established during the winter due to lower temperature.

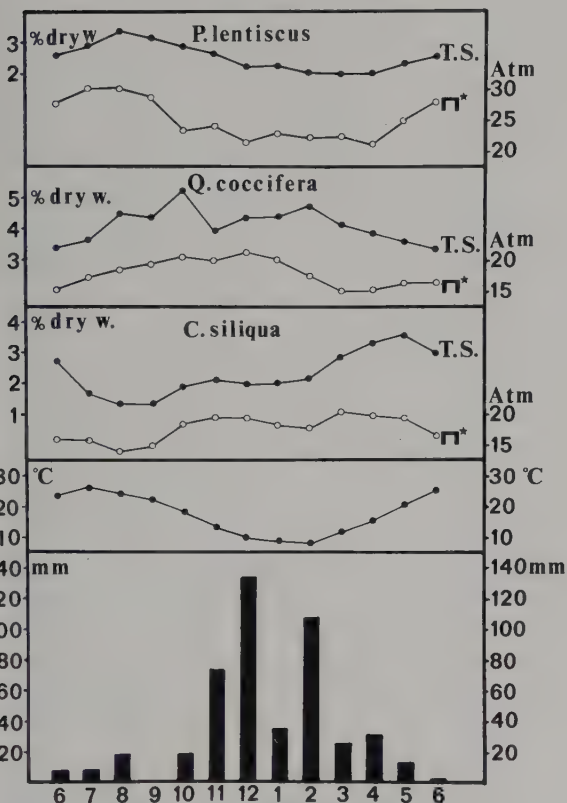


FIGURE 4. Monthly precipitation, mean monthly temperature, osmotic pressure (π^*) and total sugar content (T.S.) in the leaves of *Ceratonia siliqua*, *Quercus coccifera* and *Pistacia lentiscus*.

3.5. Total lipid content in the leaves and the bark of *Pistacia lentiscus* (Figure 5).

From the results of our measurements it appears that the physiological behaviour of the total lipids in the leaves and the bark of *Pistacia lentiscus* was opposite to that of the sugars. In the leaves during the summer we observed a

decrease while in the winter an increase of the storage lipids. A rise was also observed during the growth period in the spring.

In the bark as in the leaves the storage lipids decreased during the dry period in the summer while during the fall and the winter they increased. The maximum was observed in November and the minimum in July.

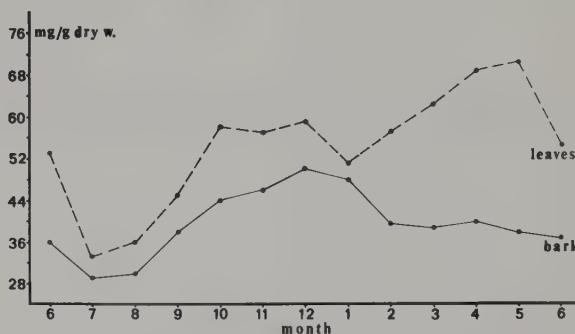


FIGURE 5. Content of total lipids in the leaves and the bark of *Pistacia lentiscus* during the course of a year (in mg/g dry weight).

3.6. Total lipid content in the leaves and the bark of *Ceratonia siliqua* (Figure 6).

As in *Pistacia lentiscus* we observed in the leaves of *Ceratonia siliqua* a decrease of the total lipids during the summer and an increase during the winter. On the contrary the bark of *Ceratonia siliqua* showed a rise of the total lipids during the summer. This high lipid content remained during the winter. In the two plants (*Pistacia lentiscus* and *Ceratonia siliqua*) the total lipid content was higher in the leaves than the bark during the whole year.

3.7. Fatty acid composition in the bark and the leaves of *Pistacia lentiscus* (Tables 1, 2).

In the bark of *Pistacia lentiscus* we determined the following fatty acids: Palmitic acid (16:0), palmitoleic acid (16:1), stearic acid (18:0), oleic acid (18:1), linoleic acid (18:2), linolenic acid (18:3), arachidic acid (20:0). There were also several fatty acids with less than 16 C atoms

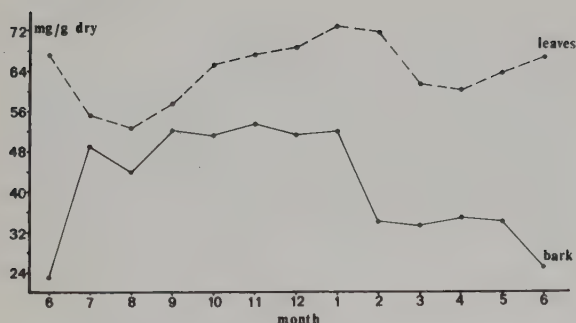


FIGURE 6. Content of total lipids in the leaves and the bark of *Ceratonia siliqua* during the course of a year (in mg/g dry weight).

present in small amounts, they were all together lumped as "lower fatty acids". The predominate saturated fatty acid was palmitic while the unsaturated was linoleic. In the leaves the fatty acid composition was almost the same as in the bark although arachidic acid was not present. Also myristic acid was found in higher amounts in the leaves and showed seasonal variations. The saturated palmitic acid predominated in the bark. Linolenic acid was the predominate unsaturated acid.

3.8. Fatty acid composition in the leaves and the bark of *Ceratonia siliqua* (Tables 3, 4).

The leaves of *Ceratonia siliqua* contained the following fatty acids: "Lower fatty acids", palmitic acid (16:0), palmitoleic acid (16:1), stearic acid (18:0), oleic acid (18:1), linoleic acid (18:2), linolenic acid (18:3). As in the leaves of *Pistacia lentiscus* the saturated palmitic acid predominated as did the unsaturated linolenic acid. In the bark of *Ceratonia siliqua* we determined the same fatty acids as in the bark of *Pistacia lentiscus*. Palmitic acid and oleic acid showed a rise during the summer while linoleic acid and linolenic acid rose during the winter.

4. DISCUSSION

The annual variations of the cellular osmotic pressure in the leaves are rather parallel to the variations of the total sugars. With the beginning of the dry summer period a rise of the total sugars was observed in *Pistacia lentiscus* and *Quercus coccifera* with a parallel increase of the osmotic pressure. In the leaves of *Quercus coccifera* the increase of the osmotic pressure continued up to December when the maximum was observed. Similar results were also obtained by Breckle, Kull (1971) in *Quercus baloot* from Afganistan. On the contrary in the leaves of *Ceratonia siliqua* we found that the total sugar content and the osmotic pressure decreased in the summer. It seems that *Ceratonia siliqua* is not affected by the drought in the summer and is more hydrostable than *Quercus coccifera* and *Pistacia lentiscus*.

In the bark the total sugar content increased during the summer and began decreasing during the fall when water became available and the activity of plants increased. During the winter the total sugar content remained low, while before the beginning of the growth period an increase of the total sugars was observed in *Pistacia lentiscus* and *Ceratonia siliqua* and then a decrease. It may be the sugars are utilized for the growth of the plants during this period. In the bark of *Quercus coccifera* the sugars remained at a low level throughout the winter and the growth phase.

In the mediterranean area the temperature of winter does not seem to affect the annual changes of carbohydrates as happens with the plants of central Europe (Jeremias 1964, 1969 and Diamantoglou 1974) and thus no increase of the sugars and no production of sugars of the raffinose group was observed. On the contrary, as U. Kull mentions (personal communication), in the leaves of *Quercus coccifera*, which grew under the climatic conditions of central Europe sugars of the raffinose group (stachiose, verbascose) were found.

The total lipid content in the leaves of *Pistacia lentiscus* and *Ceratonia siliqua* decreased during

TABLE 1. Fatty acid composition of saponifiable lipids in the bark of *Pistacia lentiscus* (as % of total fatty acids).

fatty acid	month												
	6	7	8	9	10	11	12	1	2	3	4	5	6
C 14:0	3.7	3.8	4.1	4.3	3.2	2.8	2.3	3.0	2.8	2.9	2.8	3.1	3.2
C 16:0	20.5	19.5	19.9	21.0	19.5	19.5	19.8	20.6	23.0	22.8	22.7	22.3	21.0
C 16:1	trace	trace	trace	trace	1.4	4.3	4.2	3.4	2.2	2.0	2.2	trace	trace
C 18:0	2.5	3.6	4.3	3.4	3.9	3.5	3.1	3.2	2.8	2.9	1.7	1.9	2.1
C 18:1	25.1	26.5	27.6	26.6	25.3	23.9	22.8	21.0	20.7	22.9	23.2	24.2	25.5
C 18:2	39.4	38.8	36.9	35.8	38.1	37.5	38.0	40.3	42.8	40.3	40.7	40.1	40.0
C 18:3	8.8	7.8	7.2	8.9	8.6	8.5	9.8	8.5	5.7	6.2	6.7	8.4	8.2
C 20:0	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace

TABLE 2. Fatty acid composition of saponifiable lipids in the leaves of *Pistacia lentiscus* (as % of total fatty acids).

fatty acid	month												
	6	7	8	9	10	11	12	1	2	3	4	5	6
C 14:0	3.2	3.5	3.9	4.1	4.6	5.0	5.3	4.1	2.2	2.7	2.7	3.6	3.0
C 14:0	3.5	4.0	3.8	4.6	7.2	7.8	7.3	6.1	5.8	5.4	5.0	4.6	3.9
C 16:0	21.6	22.2	21.8	21.4	22.4	22.2	17.9	18.2	19.3	20.2	19.9	21.4	22.8
C 16:1	1.4	1.3	1.2	1.2	1.8	1.9	1.4	1.1	0.9	0.8	0.8	1.2	1.6
C 18:0	1.7	1.9	1.4	1.4	1.5	2.0	1.7	2.1	2.1	2.0	2.0	2.5	1.9
C 18:1	15.2	20.8	22.7	19.6	13.7	10.8	8.3	8.2	9.8	10.0	10.1	10.7	13.6
C 18:2	16.0	12.6	10.3	12.5	14.0	14.8	18.1	21.1	21.2	21.0	21.2	18.6	16.6
C 18:3	37.4	33.7	34.9	35.2	34.8	35.5	40.0	39.1	38.7	38.3	38.3	37.4	36.6

TABLE 3. Fatty acid composition of saponifiable lipids in the leaves of *Ceratonia siliqua* (as % of total fatty acids).

fatty acid	month												
	6	7	8	9	10	11	12	1	2	3	4	5	6
C 14:0	10.6	13.0	12.6	10.9	9.2	14.3	6.8	6.1	3.9	3.4	7.7	7.5	9.6
C 16:0	19.7	25.2	28.7	25.6	25.1	17.7	21.5	19.5	19.4	17.9	18.3	17.9	18.1
C 16:1	1.2	1.6	trace	trace	trace	trace	trace	trace	0.9	0.5	0.8	0.9	0.8
C 18:0	5.1	4.9	6.0	4.7	4.9	3.9	4.1	4.5	4.4	4.6	4.2	4.1	3.8
C 18:1	9.3	14.6	14.4	15.4	14.8	8.6	5.9	5.8	5.1	4.2	4.9	6.6	6.1
C 18:2	9.9	10.3	8.4	8.4	9.4	12.3	11.8	11.7	13.5	12.5	10.2	11.3	10.9
C 18:3	42.9	29.5	28.4	33.3	34.9	41.4	48.2	50.6	51.2	54.4	51.9	50.3	49.6
not identified	1.3	0.9	1.5	1.7	1.7	1.8	1.7	1.8	1.6	2.5	2.0	1.4	1.1

TABLE 4. Fatty acid composition of saponifiable lipids in the bark of *Ceratonia siliqua* (as % of total fatty acids).

fatty acid	month												
	6	7	8	9	10	11	12	1	2	3	4	5	6
C 14:0	6.3	8.4	7.4	6.2	8.3	5.0	4.5	4.9	5.4	4.9	5.2	4.7	6.9
C 16:0	34.4	33.7	27.8	30.7	28.1	25.5	25.5	24.1	25.5	23.3	25.2	26.6	33.3
C 16:1	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace
C 18:0	9.5	9.1	4.1	7.2	6.7	6.0	6.7	7.3	6.8	7.9	9.1	7.2	8.7
C 18:1	16.9	17.4	18.4	19.8	18.3	18.1	14.1	14.5	13.3	11.7	12.5	13.0	15.9
C 18:2	15.1	14.3	26.6	23.5	23.4	28.6	33.7	32.6	26.9	27.4	26.9	26.6	16.0
C 18:3	9.9	9.7	9.3	8.1	10.2	11.8	15.5	16.6	22.1	24.8	18.1	17.1	12.0
C 20:0	7.9	7.4	6.4	4.5	5.0	5.0	trace	trace	trace	trace	3.0	4.8	7.2

the summer. It may be the lipids were utilized during the dry period in the summer or it may be they were converted into carbohydrates and thus the high osmotic pressure of the leaves resulted. During the winter a rise of the storage lipids was observed in the mediterranean plants that is due to the nongrowth phase of the plants rather than to the effect of temperature. Larcher et al. (1973) note that in plants in which no rise of the total sugars is observed during the winter, due to the climatic conditions, most of the storage substances are stored in the form of lipids. In the leaves of *Pistacia lentiscus* the storage of lipids is high during the main growth period in the spring. A second growth period was observed for these plants from September to November. In the bark of *Pistacia lentiscus* the total lipids decreased during the main growth period and continued decreasing throughout the summer. In contrast *Ceratonia siliqua* showed a rise of the storage lipids during the summer. The low content of storage lipids in the bark of *Pistacia lentiscus* may be due to the high temperature and the drought during this period.

The fatty acid composition in the leaves and the bark of *Pistacia lentiscus* and *Ceratonia siliqua* was similar. During the winter an increase of the polyunsaturated fatty acids was observed that is apparently due to the low temperature during this period (see also Appelquist 1971,

Kull, Jeremias 1972 and Hofaecker-Klett, Beringer 1975). The saturated fatty acids increased during the hot period in the summer. In the leaves of *Pistacia lentiscus* the content of myristic acid was higher than in the leaves of *Ceratonia siliqua* or in the bark of either species.

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PART THREE

STAND PRODUCTIVITY

While information on the productivity and biomass of forest communities have long been available due to economic interest in such areas, it is only recently that comparative studies on Mediterranean-type ecosystems have been carried out. These first studies, most of which were completed in the last decade, have clearly documented the extreme range of biomass structure and productivity which may be present in Mediterranean-climate shrublands and forests. Evergreen oak forests in southern France contain nearly 270,000 kg ha⁻¹ of above ground biomass (Loissant, 1973) while a mature Greek phrygana community has only about 10,000 kg ha⁻¹ (Margaris, 1975). Despite this tremendous range of above ground biomasses, the net above-ground primary production (NPP) for the range of broad-leaved Mediterranean-climate communities which have been studied all fall within a relatively small range of about 3400-6500 kg ha⁻¹ yr⁻¹. These latter data provide a basis for many ongoing studies on the controlling factors of NPP in the range of Mediterranean-climate ecosystems which occur in the world today.

Five such studies are included in the following section, covering a divergent range of Mediterranean community types.

The relationship between fire and patterns of post burn recovery of productivity are dealt with in case studies from two communities. Arianoutsou-Faraggitaki and Margaris document the regeneration of Greek phrygana ecosystems following fire. In these careful studies of the first two years of regrowth of both resprouting and reseeded species they were able to compare morphological, phenological and physiological changes in these communities, as well as monitor productivity. They conclude that no more than 10 years would be necessary to restore preburn levels of NPP for their stands.

The fire studies of Rundel et al. from low evergreen communities of Chamaebatia foliolosa from California provide comparisons of post-fire and control rates of NPP and nutrient uptake. Stand productivity is enhanced in the first year of regrowth of both fall and spring burn plots in comparison to control, despite the complete destruction of living above-ground tissues by the fires. The basis for this high level of NPP in the first post-fire growing season is the high rate of nutrient uptake in resprouting plants. This is the first fire-nutrient study to carefully document this degree of nutrient-utilization in post-fire growth, reflecting the greater availability of nutrients on burn plots.

The range of factors influencing productivity and biomass accumulation in South African fynbos communities are treated broadly by Rutherford. The South African mediterranean-climate regions provide fascinating area of research with structural complexity and short burning cycles. The natural frequency of fire appears to be far greater than in comparable areas of California or the Mediterranean region. Despite the extremely poor nutrient status of fynbos soils, post-fire regrowth rates are quite high. While phrygana, Chamaebatia and many fynbos communities fall on the lower end of the scale of above-ground biomass for Mediterranean ecosystems, the Pinus pinea stands from southern France reported on by Rapp and Cabanettes

clearly represent the opposite end of the scale. These stands contain nearly $160,000 \text{ kg ha}^{-1}$ of above-ground biomass plus $21,000 \text{ kg ha}^{-1}$ of below ground tissues. With $14,300 \text{ kg ha}^{-1} \text{ yr}^{-1}$, this community is more than twice as productive as any broad-leaved evergreen community reported for Mediterranean-climate ecosystems.

Although most productivity studies of Mediterranean regions have dealt with wood communities, grasslands are important components over wide areas.

In the final paper of this section Papanastasis describes the structure and productivity of three grassland communities along an elevational gradient in northern Greece. The differing seasonal growth patterns of C^3 and C^4 grasses are apparent in this results. Outside alpine limits, we are not surprised because of the expected orographic moisture effects. (It is surprising, however, the community productivity was directly related to elevation.)

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BIOMASS AND PRODUCTIVITY OF A PINUS PINEA L. STAND.

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INTRODUCTION

Among the three most frequent pine species encountered around the Mediterranean : *Pinus halepensis*, *Pinus brutia* and *Pinus pinea*, the last has the largest areal extent. *Pinus halepensis* is found mostly in the northern and western part of the Mediterranean Basin, and *Pinus brutia* in the eastern part. Only *Pinus pinea* is found all around the Basin.

In France, *Pinus pinea* occurs naturally in the Rhone delta and as plantations on the eastern side of that river, in Provence and Cote d'Azur.

The present study characterizes the ecology of *Pinus pinea* especially the productivity and the partitioning of organic matter in a stand.

THE STUDY SITE

The forest studied is located in the Rhone delta, growing on sand dunes. The trees are 35 years old, originating from natural regeneration after a forest clearcut in 1944. At the present time the trees have a mean height of 10 - 11 m, a mean girth of 63.4 cm at breast height, and a density of 800 stems per hectare.

The soil is a regosol with little profile development, formed on calcareous sands of marine origin. It is covered by a typical moder litter layer, from 5 to 12 cm thick. The water table, fluctuates between a depth of 1 and 1.5 m.

According to the classification of EMBERGER (1955), the climate is "Mediterranean subhumid".

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BIOMASS

The aerial biomass of the stand was established by felling, measuring and weighing sample trees (CABANETTES and RAPP, 1978). The results of these measurements allowed the calculation of regression equations (Table 1) between partial or total aerial biomass and DBH or stem circumference at breast height ($C^{1.30}$). These equations have been calculated by selecting representative trees from all DBH classes in a number proportional to the number of stems in each class (CABANETTES, 1979).

Concerning root biomass, two methods have been used. The first one is similar to the aerial biomass determination : after extracting and weighing of the root system of the sample trees, occupying an area of 1.50 m of radius around the stem, the following regression equation was calculated :

$$Y = 1.71552 x + 1.23008 \quad (R = 0.980)$$

with Y = logarithm root biomass and x = logarithm circumference at breast height.

	a	b	r
Aerial biomass	2.62521	0.33501	0.996
Needle biomass	2.62178	- 0.75075	0.949
Wood biomass	2.64268	0.26353	0.997
Trunk biomass	3.09450	- 0.79388	0.971

Table 1. - Parameters of the regression equations between the circumference at breast height ($C^{1.30}$) and total or partial aerial biomass. The equation being :

$$Y_{\text{biomass}} = ax(C^{1.30}) + b$$

with Y = logarithm (biomass) ;

X = logarithm ($C^{1.30}$) ;

r = correlation coefficient

Extraction of roots from soil monoliths located between the trees, of 230 cm of surface and 80 cm of depth was also undertaken to improve the root biomass determination. The mean result of

seven samples amounted 438 g m^{-2} of roots.

From these measurements the biomass of the site was estimated to be 178.8 t ha^{-1} , which could be separated into :

156.8 t ha^{-1} aerial biomass

22.0 t ha^{-1} root biomass

The above-ground biomass was partitioned as follows :

Needle biomass 12.7 t ha^{-1}

Woody biomass 144.1 t ha^{-1}

of which 97.5 t ha^{-1} was formed by boles and 46.6 t ha^{-1} by branches.

Pinus pinea has also a standing dead biomass, consisting mainly of dead branches, remaining for up to ten years on the stem. We calculated the following regression equation between the $C^{1.30}$ (circumference at breast height) and the amount of dead material :

$$Y = 2.0554 x + 0.31389 \quad (r = 0.916)$$

which gives an estimate of the standing dead material of 11.3 t ha^{-1} .

These values may be compared with those given by RODIN and BAZILEVICH (1967). They indicated for a 33 year old *Pinus silvestris* stand, a 22 year old *Pinus nigra* stand and a 32 year old *Pinus abies* stand, the following aerial biomass values respectively : 140, 142 and 169 t ha^{-1} . RAPP (1974) estimated the above ground biomass of a 60 year old *Pinus halepensis* plantation as 157 t ha^{-1} .

The *Pinus pinea* site has a smaller biomass than other, comparable aged pine stands. The latter stands, all have higher tree densities. However when expressed per stem unit, the amounts are near the same between all of the pine stands, including *Pinus pinea*.

COZZO (1969), noted in Argentina, a volume of 8.6 m^3 *Pinus pinea* stem wood for 1 m^2 surface at breast height. In the present study, the volume was only $6 \text{ m}^3 \text{ m}^{-2}$ surface at breast height. These differences can be explained by the dissimilarity of climate. In Italy,

CIANCIO (1968) gives similar values to those we found in France for that species.

Concerning root biomass, no other values are available for *Pinus pinea*. In general, the amounts found are small, in comparison with the amounts indicated by RODIN and BAZILEVICH (1967) for other pines.

PRODUCTION OF BIOMASS

To determine the amount of biomass produced each year, we used the relation :

$$P_N = T + L_{PN}$$

in which : P_N = yearly net production

T = total production of living material during one year

L_{PN} = litter produced during the same year

The estimation of T occurs by measuring :

- the increment of xylem
- the production of bark
- the amount of one year old needles at the end of the growth period.

Xylem was determined by measuring the age rings of the sample trees and their annual volume increment during the last five years and by calculating a regression between that volume and the circumference at breast height (CABANETTES and RAPP, 1981) :

$$\log V = 2.0426 \log C^{1.30} + 0.12564 \quad (r = 0.965)$$

Using the density of the wood, 0.45 (CABANETTES, 1979) we can then calculate the amount of wood produced yearly.

Bark is estimated by the method of KESTEMONT (1977) assuming that there is the same relation of biomass/production for bark than for xylem.

During the biomass determination the one and two-year old needles were separated on four trees (CABANETTES and RAPP, 1978). The first year old needles amounted to between 52 to 58 % of the total needle mass, corresponding to a mean value of 55 %. The comparison between needle biomass

and needle litter allows the calculation of a correction factor, for the estimation of needle production during the years where litter fall was studied.

On the same sample trees, the one year shoots were also measured and the results were generalized to the site by using the DBH of the sample trees and of the stand.

The production of male flowers was directly estimated from litter fall. Concerning female reproductive organs, or cones, the three year old cones of a sample of trees were weighed and the result generalized for the stand.

For root production, we did not measure values for yearly increment of biomass, or yearly production of fine roots. We used the approach of KESTEMONT (1977) and KESTEMONT and al. (1977), based on the similarity of the production between the above ground and underground parts of the biomass :

$$\text{Root production} = \frac{\text{root biomass}}{\text{aerial perennial production}} \times \frac{\text{aerial perennial production}}{\text{aerial perennial biomass}}$$

By these approaches the yearly production was estimated to amount to 18.6 t ha^{-1} and could be divided, as indicated in table 2, into several parts.

Compared with values for other coniferous forests that have been studied, we can not that the total production is near the same as a 55 year old *Picea abies* stand from Belgium (KESTEMONT and al., 1977). The bole production of *Pinus pinea* of $3.8 \text{ t ha}^{-1} \text{ year}^{-1}$ of wood or $7.6 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ is very low (DECOURT, 1971, 1973 ; DECOURT and LEMOINE, 1969), comparable to the poorest forest stands of France. But the same productivity has been recorded for other *Pinus pinea* sites (ILLY, 1978, personal communication) in the south of France. It seems therefore that this low productivity results mostly from the climate and especially the summer dryness. COZZO (1969) noted double productivity for *Pinus pinea* in Argentina, where

the distribution of rain is more even than in the Mediterranean area.

total production 18.6	aerial 17.5 94.1 %	perennial 6.1 32.8 %	xylem 3.1 16.7 %	
			trunk 3.8 20.4 %	bark 0.7 3.7 %
			branches 2.3 12.4 %	
		reproductive 4.0 21.5 %	flowers male 0.3 1.6 %	
			cones 3.7 19.9 %	
		needles 7.4 39.8 %		
		roots 1.1 5.9 %		

Table 2. - Production of a *Pinus pinea* stand.

Amounts in $\text{t ha}^{-1} \text{ year}^{-1}$ and as percentage of the total production.

Needle production is however very high. Even if we use needle litter fall, which amounts $6.1 \text{ t ha}^{-1} \text{ year}^{-1}$, the results are about 20 % higher than the highest values indicated by BRAY and GORHAM (1964) for 20 to 50 year-old temperate or warm forests. These amounts can also be related with the age of the stand. Between 30 and 40 years, forest stands are at the peak of their productivity (LEMEE, 1974 ; DUVIGNEAUD, 1971).

The $3.7 \text{ t ha}^{-1} \text{ year}^{-1}$ of cones are high amounts against other conifers however. DJAZARI (1971) and CAPPELLI (1958) noted higher amounts for *Pinus pinea* in Italy.

The below-ground productivity is possibly greater than the $1.1 \text{ t ha}^{-1} \text{ year}^{-1}$ that we determined. That amount is only 6 % of the total productivity, while BRAY and GORHAM (1964) and RODIN and BAZILEVICH (1967) noted that root production

generally amounts to 15 % of the total production.

CONCLUSION

The biomass of a 35 year old *Pinus pinea* stand, growing along the Mediterranean coast, amounted to 178.8 t ha⁻¹, formed by 156.8 t ha⁻¹ of above-ground biomass and 22 t ha⁻¹ below-ground biomass.

Boles make up 62 % of the above-ground biomass, the branches 31 % and the needles 7 %. The proportion of the canopy material in relation to boles is very important. Small root biomass could also be important particularly in the sandy soil of the study site.

The high amounts of biomass accumulated yearly results especially from the high needle production (7.4 t ha⁻¹). But the production of wood, expressed as volume, seems low, compared to other coniferous species.

Pinus pinea appears to be a species with a good potential to grow and to colonize the coastal zone of the Mediterranean, particularly those areas formed by sand dunes having a water table with low salinity. The high productivity of *Pinus pinea* allows also this species to be, not only an ornamental tree, producing shade around houses and in touristic areas, but also a tree of economic importance for forest production.

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BIOMASS STRUCTURE AND UTILIZATION OF THE NATURAL VEGETATION IN THE WINTER RAINFALL REGION OF SOUTH AFRICA

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1. INTRODUCTION

Several ecological and plant geographical aspects of the vegetation of the winter rainfall part of the Cape Province of South Africa have been recently reviewed by Taylor (1978), Kruger (1979), Day et al. (1979) and Boucher, Moll (in press). This paper does not aim to repeat their broad coverage, but intends to expand on selected aspects of biomass structure and utilization of the vegetation in and adjacent to the winter rainfall area.

The area of winter rainfall (more than 60% rain in the winter half-year), of summer rainfall (more than 60% rain in the summer half-year) and the intermediate zone of rain throughout the year are indicated for the Cape in Fig. 1.

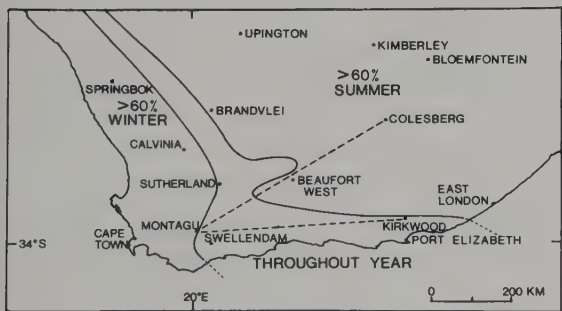


FIGURE 1. Areas of winter rainfall and summer rainfall (as percentages of mean annual rainfall) and rain throughout the year in the Cape Province. Straight dashed lines indicate transects referred to in the text.

The proportion of rain in the winter half-year increases to almost 90% at, for example, Citrusdal (Taylor, 1977). The local Department of Agriculture and Fisheries recognizes as one of its agricultural regions the 'Winter Rainfall Region' that also includes much of the area with rain throughout the year. The Region

has a prominent folded mountain belt that runs north-south in the western parts and turns east-west in the southern parts. The belt separates coastal forelands from a generally arid interior but with isolated parts of the belt falling altogether within this arid interior area, called the Karoo. Soils of the mainly sandstone mountains are usually low nutrient status skeletal lithosols, whereas those of the coastal forelands (except coastal sands) and interior plains are often heavier soils with higher nutrient status. Mean annual rainfall ranges from below 100 mm in parts of the arid interior and northern parts of the west coast to over 3 000 mm in mountains near Stellenbosch. Precipitation is likely to be much augmented by winter and summer mist on the mountains (Nagel, 1962) and fog on the west coast. Short-lived snowfalls occur on the higher mountain peaks in winter. Extremely strong winds can persist, particularly in summer, for as much as 10 days (Taylor, 1978).

The vegetation of South Africa has been classified in 'veld type' units and mapped (Acocks, 1975). The veld type concept is utilization orientated and is defined as a unit of vegetation whose range of variation is small enough to permit the whole of it to have the same farming potentialities. The veld types of the winter rainfall area as defined in Fig. 1 and south of 31°S are listed in Table 1 with areas they cover in the Cape Province (Edwards, 1974). In the winter rainfall area there are: one arid coastal veld type (Strandveld), three arid inland types (Karroid Broken Veld, Succulent Karoo and Western Mountain Karoo), two Renosterbosveld types and essentially two Fynbos types. Seven of these veld types are geographically related along a simplified sequence from the coast near Malmesbury north of Cape Town to near

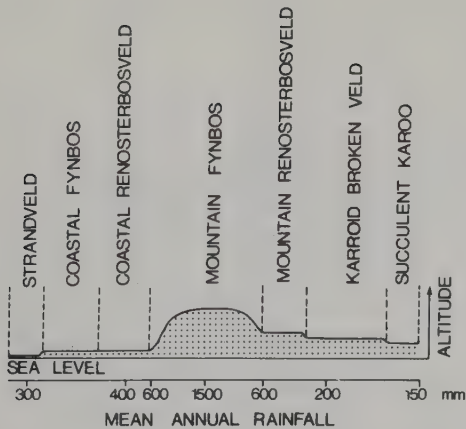


FIGURE 2. Schematic sequence of winter rainfall area veld types from the coast near Malmesbury to the vicinity of Laingsburg, indicating relationships with topography and mean annual rainfall (not to scale).

Laingsburg in the interior (Fig. 2). Although this sequence serves to illustrate common geographical, topographical and precipitation relationships between veld types, there are many examples of incomplete sequences or missing

TABLE 1. Veld types of winter rainfall area south of 31°S with areas they cover in the Cape Province (Edwards, 1974)

Veld type	Area (km ²)
Mountain Fynbos:	
Macchia	17846
False Macchia	17866
Karroid Broken Veld	33 853
Succulent Karoo	33 178
Western Mountain Karoo	19 744
Coastal Renosterbosveld	14 592
Mountain Renosterbosveld	11 172
Coastal Fynbos	8 379
Strandveld	6 308

elements owing to topographical and other variation. Subsequent descriptions of biomass structure and utilization are related to these veld type units. Temperate forest areas of the southern Cape and mountain ravines are not discussed.

2. CHARACTERIZATION OF THE VEGETATION

The vegetation of most veld types of the Cape winter rainfall area is primarily evergreen shrubland or heathland. Diagnostically important are evergreen cupressoid phanerophytes or sometimes deciduous dwarf phanerophytes in non-karroid shrublands, evergreen aphyllous hemicryptophytes in heathland (illustrated, Boucher, Moll, in press) and perennial succulents in karroid areas.

Fynbos vegetation has several properties in common with most other Mediterranean-type climate vegetation. The fynbos types contain evergreen sclerophyllous shrubs with many small-leaved species. Leaves generally have a high weight to area ratio (Cody, Mooney, 1978). Aboveground parts of plants are susceptible to fire. This is probably enhanced by presence of aromatic compounds and essential oils which also occur in some plants of the more arid veld types, for example, the Renosterbosveld types. Plant productivity is similar to that of other Mediterranean-type climate vegetation (Cody, Mooney, 1978). Habitat is subject to a maritime influence and lies at roughly 35° latitude on a generally western facing part of the continent and includes an area of winter rainfall with summer drought. Fynbos lies in relatively close proximity to semi-desert vegetation as do other Mediterranean-type vegetations. Despite such similarities in vegetation type and location between different Mediterranean-type climate areas, it has been suggested that it is purely chance that some heathlands exist today within the region of Mediterranean-type climate (Specht, 1979).

Of particular interest are the characteristics of South African Mediterranean-type vegetation that distinguish the mainly fynbos vegetation from vegetation of other Mediterranean-type areas. Several such characteristics have been identified by Cody and Mooney (1978) relative to other Mediterranean-type areas with the exception of

the Australian Mediterranean-type areas. These and other probable differential characteristics are listed, which together with the above mentioned features common to Mediterranean-type vegetation, assists in defining the important attributes of fynbos and sometimes of adjacent veld types. The characteristics include: Restionaceae, almost leafless stem-chlorophyllous graminoid herbs, dominant or important; soils with particularly low nutrient status (Cody, Mooney, 1978); most diverse structure with a whole series of dominant shrubs of different heights (Cody, Mooney, 1978); extreme variation in leaf sizes of woody dominants (Cody, Mooney, 1978); complex and prolonged successional relationships after fire; very few trees (Moll, McKenzie, McLachlan, 1980); high representation of bulbous plants (Cody, Mooney, 1978); highest average evergreen specific weights (32 mg cm^{-2}) and lignin contents (15%) of samples taken by Cody and Mooney (1978), possibly together with Australia; lowest phosphorous (0,03%) and nitrogen (0,6%) contents of leaves analyzed by Cody and Mooney (1978); no major changes in vegetation structure with a greater than tenfold change in mean annual rainfall (Kruger, 1979); co-dominance - lack of single species dominance (Taylor, 1978) - although there are important exceptions; particularly high gamma and delta floristic diversities (Kruger, Taylor, 1979); high degree of endemism relative to the Cape floral region (Taylor, 1972); possibly the occurrence of dioecious plants in groups commonly dominant, for example, Restionaceae and Leucodendron; most invaded by exotic woody species, mainly from Australia (Cody, Mooney, 1978); stronger maritime influence (Cody, Mooney, 1978) (except along the inland margin ?); exceptionally large sources of nectar (Cody, Mooney, 1978); presence of succulents (together with Chile) (Cody, Mooney, 1978); mature vegetation poor in annuals (together with California)(Cody, Mooney, 1978);

growth and flowering activity sometimes out of phase with seasons of favourable temperature and moisture (Kruger, in press), apparently also in southern Australia (Cody, Mooney, 1978). For example, Protea species generally grow from late winter to early summer but Leucodendron and Leucospermum species usually in summer and autumn (Kruger, in press). Vegetative growth of the renosterbos (Elytropappus rhinocerotis) occurs in late summer in the western Cape (Levyns, 1956) when atmospheric moisture availability is minimal.

The renosterbosveld types, found on heavier soils, are dominated by Elytropappus rhinocerotis shrubs which, in contrast to woody plant species in the other veld types, can often form almost monospecific stands. Although often apophytic after disturbance to vegetation, the renosterbos is a natural constituent of the vegetation and forms stable communities particularly in the Mountain Renosterbosveld type. Mountain Renosterbosveld in the Winter Rainfall Region is commonly a transitional vegetation type between fynbos and karroid types and has been likened to similar communities in other Mediterranean-type areas, for example, the sage communities in parts of California (Rutherford, 1978a).

The karroid types of the Winter Rainfall Region have as one of their most important features, the high frequency of succulent plants. Werger (in press) states that succulent species of the arid west coast and interior of the winter rainfall area contribute at least 30% of the flora whereas their contribution to the flora in the summer rainfall interior is about 5 to 10%. He points to findings (Mooney et al., 1977) that suggest that the majority of succulent plants from the winter rainfall area and area of rain throughout the year have the CAM (Crassulacean Acid Metabolism) photosynthetic pathway while values for succulent plants from the summer rainfall area have indicated a more even distribution between CAM, intermediate

and C₃ type plants. In the Karroid Broken Veld type occurrence of photosynthetic pathways expressed as percentage contribution to the local vegetation cover gave 49% C₃ plants, 2% C₄ plants and 49% CAM plants (Werger, in press). Werger and Ellis (in press) suggest that effects of frequent fog in supplying a regular moisture supply, low temperatures during the growth season and the decreased frost occurrence, relate to the preponderance of succulents and the CAM photosynthetic pathway in the karroid parts of the winter rainfall area. An important feature of succulence in karroid types appears to relate to increased plant community stability. Joubert (1970) and Olivier (1966) state that under either grazing conditions or complete protection, succulence results in a particularly stable community condition in the Karroid Broken Veld type.

3. BIOMASS STRUCTURE AND DISTRIBUTION

3.1. Aboveground

3.1.1. Plant community height relations. Vegetation structure has been studied in more detail in the relatively undisturbed Mountain Fynbos. Although important factors affecting occurrence of floristically defined plant communities include, for example, soil depth, moisture content and rock cover for fynbos communities on Table Mountain, Cape Town (Laidler, et al., 1978), it is not always clear to what extent such factors affect plant community biomass structure. One determinant of plant community structure is aspect, where, for example, at upper altitudes on Rooiberg, southeast of Ladismith, the polar aspect slopes bear a tall (1.5 to 2.0 m) dense mesic proteoid fynbos whereas the equatorial aspect slopes bear a low (<0.5 m) dense restioid narrow-leaved fynbos (Taylor, 1979). Although effects of elevation are a function of many variables, there is a rough correlation be-

tween elevation and plant community structure. Lower slopes often have tall proteoid shrubs, with a shorter ericoid form on the upper slopes while (low) restioids often dominate exposed ridges and summits with a reported rudimentary alpine-type flora including decumbent shrubs on some of the highest peaks (Taylor, 1978). Thus on the lower slope of the Riviersonderend Mountains south of Worcester, *Protea laurifolia* community height was 1.5 to 2.5 m whereas that of the restionaceous summit community was 0.8 m (Rutherford, 1978a). Rainfall appears to be less important in determining plant community height within Mountain Fynbos. Kruger (1979) found height of graminoid herbs (mainly Restionaceae) exceeded 1 m (above average) in both an extremely high rainfall mountain area (3 300 mm year⁻¹) near Stellenbosch and in arid fynbos areas (<400 mm year⁻¹). An inverse relationship between canopy volume of shrubs and herbs is expected from the complimentary nature of these components. However, an inverse relationship also appears to hold in mountain fynbos between canopy volume of shrubs more than 1 m height and that of the graminoid herb group (mainly Restionaceae), both as proportions of total community canopy volume (after Kruger, 1979). The presence of a relatively high proportion of obligate seed regenerators after fire (van der Merwe, 1966; Moll et al., 1980) together with long periods from germination to seed set (commonly more than 5 years in some Proteaceae) and greater frequency of fire, often results in lowering fynbos community height, preventing many plants of potential tree stature becoming established and controlling height related successional stages. In an ideal tall heathland or scrub fynbos community, tall shrubs only emerge and adopt an ascending branch habit 4 or 5 to about 10 years following fire (Kruger, 1979). Karroid Broken Veld community height varies from 0.5 to 1.0 m and sometimes locally attains 3.0 m (Joubert, 1970). This height range is similar to that in several fynbos types.

TABLE 2. Total canopy cover for selected vegetation types in the winter rainfall area

Vegetation type	Site details	Total canopy cover (%)	Source
Mountain Fynbos	35 year old tall closed-herbland communities, Dwarsberg, Stellenbosch	95 - 98	Kruger, 1979
"	18 year old low open <u>Erica corifolia</u> - <u>Restio egregius</u> community, Jakkalsrivier, Grabouw	80	Kruger, 1979
"	Whole	>70	Taylor, 1978
Arid Fynbos	±20 year old <u>Leucodendron pubescens</u> community, Langfontein, Clanwilliam	±40	Kruger, 1979
"	Community near Wupperthal	33 - 45	Taylor, 1978
Karroid Broken Veld	Localized dense <u>Euphorbia mauritanica</u> - <u>Pteronia paniculata</u> in Robertson Karoo	91	Joubert, 1970
"	<u>Crassula rupestris</u> community in Robertson Karoo	44	Joubert, 1970
Strandveld	Community near Lamberts Bay	44	Joubert, 1970

3.1.2. Canopy cover in veld types. Comparative canopy cover values for various vegetation types are Given in Table 2. Cited canopy cover values vary from about 100% to 33%, but the canopy cover in true Succulent Karoo Veld Type may be

expected to be considerably lower. Other data of Kruger (1979) suggest that in Mountain Fynbos canopy cover is more sensitive to differences in mean annual rainfall than is mean community height.

TABLE 3. Biomass of selected vegetation types in the winter rainfall area

Vegetation	Location	Age (where known) (years)	Dry mass (kg ha ⁻¹)	
Mesophyllous Mountain Fynbos	Stellenbosch and adjacent districts	2 - 5	2000 - 8000	¹
"	"	6 - 7	6000 - 16000	¹
"	Worcester district	14 - 15	11000	²
"	Stellenbosch and adjacent districts	10 - 17	13000 - 26000	¹
Mesophyllous Mountain Fynbos (biomass live)	Stellenbosch district	21	35000	³
"	"	37	23000	³
Mountain Fynbos heath	Stellenbosch and adjacent districts	3.5 - 4.5	5000 - 9000	¹
"	"	16	11000 - 15000	¹
Restionaceous Mountain Fynbos	Worcester district	-	14000	²
Mountain Renosterbosveld	"	-	11000	²
Karroid Broken Veld (succulent form)	"	-	7000 - 8000	²

¹Kruger (1977), ²Rutherford (1978a), ³van Wilgen (in press)

3.1.3. Plant biomass. Plant biomass distribution in fynbos vegetation and the adjacent arid zone has been briefly reviewed in Rutherford (1978b) with the most extensive data being that of Kruger (1977) for fynbos communities. Biomass data for selected communities are given in Table 3. Aboveground biomass is clearly dependent on time since last fire (Kruger, 1977; van Wilgen, in press). Biomass increases steadily with age till roughly 20 to 30 years is reached after which biomass (live) decreases with plant senescence. It is in this last period that fuel loads attain a maximum (van Wilgen, in press) making very intense fires possible. A similar pattern occurs in European heathlands (Gimingham, et al., 1979) but with lower maxima than in fynbos.

Work on plant biomass along an altitudinal gradient on the Riviersonderend Mountains, Worcester, did not show a significant biomass difference within fynbos at different elevations, but biomass of lower elevation Karroid Broken Veld vegetation was significantly less than

that of the fynbos of the mountain summit (Rutherford, 1978a). Biomass of the Restionaceae - Cyperaceae - Gramineae group varied directly with elevation, and mass of dead plants varied inversely with elevation along the Karroid - Renosterbos - Protea - Restionaceae elevational gradient. The increasing proportion of mass of dead plants possibly corresponds to successively harsher habitats. The common persistence of old flower heads on, for example, several Protea plants over years (usually with slow release of seed) can also result in a relatively high accumulation of dead material mass on the plant.

Production of generative reproduction structures in fynbos vegetation is increasingly being studied, mainly owing to the commercial interest in wild flowers (see section 4.3). Examples of typical production values for various units of generative reproductive structures are given in Table 4. The annual production data of flower heads per plant are valid for the age span of optimal flowering. Several species, for example, Protea magnifica and Leucospermum tottum, after

TABLE 4. Annual production of generative reproductive structures in fynbos

Species	Flower heads per plant	Florets per head	Viable seeds per head	Mean mass of seed (mg)	Source
<u>Protea cynaroides</u>	10	120-160	80	44	Vogts, 1977c
<u>Protea compacta</u>	20	-	-	-	Roux, 1979
<u>Protea repens</u>	20 - 25	-	-	-	Roux, 1979
<u>Protea magnifica</u>	25 - 50	350	30	250	Vogts, 1977a
<u>Leucospermum vestitum</u>	>50	-	-	100	Vogts, 1979
<u>Protea neriifolia</u>	20 - >100	250-400	50	32	Vogts, 1977a
<u>Leucospermum cordifolium</u>	50 - 100	-	5 - 50	125	Vogts, 1979
<u>Leucospermum tottum</u>	>100	-	-	71	Vogts, 1979
<u>Protea grandiceps</u>	-	>600	100	25	Vogts, 1977a

commencing full flowering only continue for about 5 years after which production declines. Some other species, for example, Protea neriifolia (Vogts, 1977a) and Protea grandiceps (Roux, 1979) appear to steadily increase flower head production long after that of other species has markedly decreased. In some obligate seed regenerator species with a relatively short duration of flowering, therefore, the frequency of fire may not only be too high for re-establishment of the species but may also be too low for continued effective re-seeding of the area and population expansion. Given the often great size and mass of the flower heads of several Protea species, the proportion of mass allocated annually to generative reproduction may be relatively high in shrubs with high flower head production. Data in Table 4 suggest a possible inverse relation between seed number per flower head and mean mass of seeds for a species set which in turn might reflect the limited resources of the plant.

Fruit production of a successful fynbos invader from Australia, namely Hakea sericea has been determined for a 10 year old stand of average density in fynbos near Villiersdorp (Fugler, 1979). Mean fruit crop was 532 per plant (standard error 29) and 725648 per ha for this site. Seed release from the woody fruit-follicles (two per fruit) usually occurs after fire or death of the plant. Therefore, after fire, a high level of fruit production per unit land area together with high percentage germination, promotes an expanding population.

3.1.4. Rock cover, mean slope and plant biomass. In the area of the Cape folded mountains, surface rock cover is common. It has been shown (Laidler et al., 1978) that floristic delimitation of communities on, for example, Table Mountain can be strongly influenced by rock cover. However, surface rock cover can be

very important in reducing area for plant biomass. Biomass has usually been determined in areas with limited surface rock cover and these data applied to a whole mountain can overestimate biomass. But surface rock cover may also increase moisture runoff to adjacent soil and plants by acting as a condensation surface for mist. Percentage surface rock cover has been determined for several areas for surface rock with pieces >0,5 m across (F. Ellis, personal communication). In the rugged Hex River Mountains between Worcester and Ceres, percentage surface rock varies from 40 to 60% on the south side and from 60 to 80% on the north side, while sections of the Skurweberg, north of Ceres, have an average surface rock cover of 80%. On less rugged mountains east of Clanwilliam, percentage surface rock is usually less than 30% while on the coastal forelands east of Ysterfontein, percentage surface rock is negligible (<1%). From these data it appears that plant biomass on an area basis may be expected to be much reduced through surface rock in many mountain areas of the Western Cape.

Slope is also potentially important in Mountain Fynbos. Work relating slope angles to occurrence of Aloe ferox and fynbos vegetation has suggested that land plants growing in mid-latitudes are often restricted to ranges of a particular and narrow range of slope angles (Holland et al., 1977). Slope, however, also increases surface areas over horizontal map areas. Biomass values determined per unit surface area on a slope may, if applied to a whole mountain's plan area, underestimate biomass. This has implications for resource planning and management of very steep areas. Mean percentage slopes have been determined for various areas of the western Cape (F. Ellis, personal communication). East of Clanwilliam, mean slope varies from 20 to 40% whereas in the Hex River Mountains between Worcester and Ceres the mean varies between 60 and 90%. When these values are converted to surface area increases over

horizontal map areas, the first area increases in area by 2 to 8% and the second by 17 to 35%. In the coastal forelands east of Ysterfontein, mean slope between 0 and 6% results in no effective increase in surface area. In terms of total biomass resource of the cited mountain regions, it appears that the effect of slope in increasing area may be offset by reduced production on poorer soils of steeper slopes. But even if not, the effect of increased surface area through slope is altogether cancelled by the effect of reduction of soil area by surface rock in the areas considered.

3.2. Belowground

Studies of belowground plant biomass in the winter rainfall area have been very limited and have presented particular difficulties of access in the rocky substrate in areas of Mountain Fynbos. In fynbos, not only do roots of plants occur belowground but sometimes the majority of the main (unbranched) stem. Thus in Leucospermum cuneiforme a subterranean main stem (lignotuber) has been reported (Vogts, 1979) while in Protea magnifica, the main stem is usually below the soil surface (Vogts, 1977a). In Protea cynaroides the main stem is usually partly or totally covered with blown soil (Vogts, 1977c). The distribution area of this species (and most others) is subject to light to gale force winds with light wind (5 to 14 km hour^{-1}) continuing for usually a week before strengthening again. Even in sheltered ravines a full day with $<3,6 \text{ km hour}^{-1}$ wind is unusual (Vogts, 1977b). The effect of wind force on many fynbos plants is reduced by the common low growth habit, but rooting habits and anchorage effectiveness vary. In some species of Proteaceae, for example, Protea grandiceps and P. cynaroides the tap root is particularly well developed and this together with well developed less superficial horizontal roots anchors plants of these species very firmly and resists wind

(Vogts, 1971; 1977a). In other species, such as Protea neriifolia, roots do not grow straight down for more than 300 mm and there is a preponderance of shallow laterals (Vogts, 1977a). Root systems of Leucospermum cordifolium, L. cuneiforme, L. tottum and L. vestitum consist of thick deep-growing roots with a network of shallow, spreading, thin roots (Vogts, 1979).

The average width (3 m) of the whole root system of the mature Protea cynaroides plant is more than twice the average depth (1,1 m) (Vogts, 1977c). However, this species is not as dependent on great depths as on spaces between rocks in its natural environment. Where roots grow through narrow passages or cracks in rocks, they re-thicken where space is available, but this root thinning and thickening also occurs in soil without rocks and is unrelated to pathological thickening caused by nematodes (Vogts, 1971). Roots of Protea magnifica under natural conditions of rocks and stones necessarily distort but the distorted roots have also been found in cultivated plants (Vogts, 1977a) presumably under uniform soil conditions. Under natural shallow soil conditions with impervious substratum, roots of Protea neriifolia extend horizontally and the tap root may turn almost rectangularly just below the surface of the soil. This ability may correlate with this species tolerance of poorly-drained subsoil (Vogts, 1977a). In Othonna cacalioides, a dwarf succulent of the Succulent Karoo veld type, growing on very shallow soil, roots have been reported to radiate partly aboveground for 0,5 m before being firmly anchored (Hall, 1974).

Proteoid type roots, the dense clustering of extremely hairy rootlets, are probably normal components of root systems in the Proteaceae of southern Africa (Lamont, 1980). Such roots are probably of great importance for nutrient uptake in the nutrient poor soils of the fynbos areas and for store of surface water (Lamont, 1980)

possibly also during summer mist conditions. Jooste et al. (1980) report that, in Leucospermum salignum, the uptake of sodium and potassium by proteoid roots was approximately twice that by normal roots. Proteoid roots are indicated to be exceptionally prominent in Protea magnifica (Vogts, 1977a).

Under experimental conditions, root growth of young plants of Protea cynaroides was found to complete before shoot growth commenced in two successive growth flushes (Hanekom, 1971). Root growth took place at times when day and night temperatures decreased for varying periods.

4. Plant biomass utilization

4.1. Overview

Land use within the Winter Rainfall Region, long before colonial settlement in the seventeenth century, involved exploitation by Khoisan tribes of timber for firewood and firing the vegetation to improve forage production (Werger et al., 1972). Since the seventeenth century, these and other activities greatly increased and the lowlands, particularly the Coastal Renosterbosveld type, have largely been converted to wheatlands, plantings of grape vines or deciduous fruits. The Mountain Fynbos has not greatly changed but pine plantations have been established in some areas and woody pest plants such as species of Hakea are colonizing extensive areas. The karroid areas have over the last two centuries experienced heavy overgrazing by small stock, a position aggravated by the unsuitability for free ranging stock of most other veld types in the region. Natural mammal populations have diminished or disappeared as a result of hunting and destruction of habitats in the surrounding lowlands (Werger et al., 1972). It is estimated that man's impact on the extremely rich flora of the south western Cape has been severe and

only 39% of its former natural area remains (Hall, Boucher, 1977). In historical times, records show Protea nitida trees with DBH of 600 mm whereas today trees with a DBH of more than 300 mm are exceptional (Moll et al., 1980).

Current utilization of natural plant biomass in the Winter Rainfall Region involves both direct and indirect biomass utilization. The indirect uses involve manipulation of the plant biomass for management purposes. Such purposes include: increasing run-off of water in mountain catchments by controlled burning of plant biomass (Wicht, 1971); maintaining and promoting floristic and vegetational diversity for recreational and scientific needs by various conservation policies; and reducing wild fire hazards by timeous burning. Direct uses of plant biomass are more clearly linked to economics. The two economically most important biomass uses are that of natural grazing for small stock production and wild flower production particularly in fynbos areas. These two aspects will be discussed in following sections. Other direct uses of biomass include: production of Rooibos tea, from the endemic indigenous shrub Aspalathus linearis in the Clanwilliam fynbos area where annual tea production exceeds 2 000 000 kg (Edwards, 1976); production of Buchu, also an endemic indigenous shrub (Agathosma betulina) from fynbos at Clanwilliam that is used to supply one of the world's most expensive volatile oils to the pharmaceutical industry (the 1970-71 harvest produced about 10 000 kg of the oil, Edwards, 1976); widespread provision of high quality thatching material from various species of Restionaceae, for example, Thamnochortus insignis (Rourke, 1974); and various other special local uses, for example, extract of tannins from, for example, Colpoön compressum.

4.2. Grazing

The grazing potential for small stock of the natural vegetation of the Winter Rainfall Region is low.

Most grazing is obtained from cultivated fields and is only supplemented from natural vegetation (F. du Toit, personal communication). Although areas of fynbos are patch-burnt particularly on lower mountain slopes to stimulate new palatable growth, including that of Restionaceae in the early stages Kruger, Bigalke, in press), the grazing value of this vegetation is so low that alternative uses of it have been recommended (le Roux, 1966). The predominance of generally unpalatable Restionaceae at the cost of Gramineae in fynbos is reflected in ratios of Restionaceae to Gramineae canopy cover in undisturbed communities. Such ratios range from zero in Karroid Broken Karoo through 0.2 to 0.3 for both Renosterbosveld types and 0.6 in Strandveld to 1.2 in Coastal Fynbos and 2.6 in one area of Mountain Fynbos (van Rensburg, 1962; Joubert, 1971). More than half the typical fynbos communities, given by Kruger (1979), have ratios of greater than 5 indicated. These values drop sharply after disturbance through fire or clearing, owing to an increase in grass. Fynbos vegetation is utilized to a certain extent by wild animals, for example, nectar feeding field mice (Wiens, Rourke, 1978).

The proportion of plant cover that is edible in

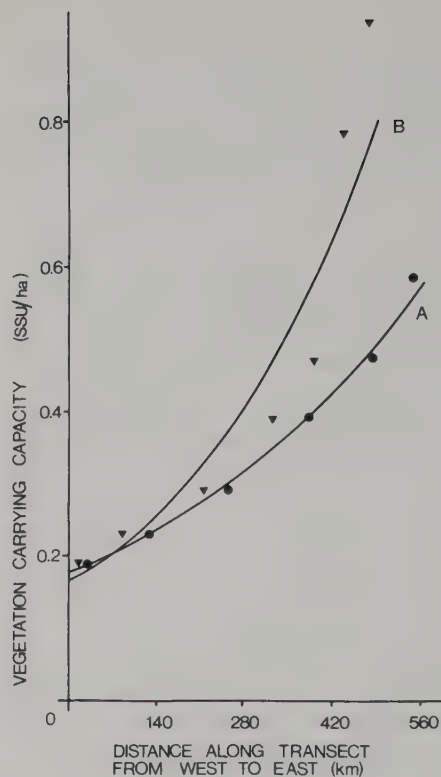


FIGURE 3. Relationship between a winter-summer rainfall area gradient and carrying capacity of the vegetation for (A) a more arid transect (Montagu - Colesberg) and (B) a more mesic transect (Montagu - Kirkwood). SSU is small stock unit

TABLE 5. Chemical composition (moisture-free basis) of composite samples of edible plants in July per veld type (after Joubert et al., 1969; Stindt, Joubert, 1979; Joubert, Stindt, 1979)

Veld type	Fibre (%)	Protein (%)	Ash (%)	P (%)	Ca (%)	Mg (%)	Mn (ppm)	Fe (ppm)	Cu (ppm)
Mountain Fynbos	31.25	4.51*	6.04	0.05*	0.25	0.16	93.2	450	9.8
Coastal Fynbos	29.31	5.83*	10.89	0.06*	0.40	0.17	76.6	682	8.7
Mountain Renosterbosveld	36.11	5.22*	6.54	0.04*	0.27	0.12	67.8*	838	8.7
Coastal Renosterbosveld	31.01	5.99*	10.07	0.05*	0.24	0.16	94.7	882	9.1
Karroid Broken Veld ⁺	26.80	8.69	11.54	0.09*	0.96	0.48	247.4	435	6.0*
Succulent Mountain Scrub	26.82	9.41	10.72	0.12*	0.87	0.37	136.7	1044	9.5

* Nutrient deficient for grazing animals as indicated by Stindt et al., (1965)

⁺ Analyses of only the most common vegetation variations included

TABLE 6. Chemical composition (moisture-free basis) of individual plant species

Species	Fibre (%)	N (%)	Pro- tein (%)	Ether extract (%)	NFE (%)	Ash (%)	P (%)	Na (%)	K (%)	Ca (%)	Mg (%)
<i>Protea cynaroides</i> ¹ (Mountain Fynbos)		0.69	4.31*				0.034	0.40	0.12	1.12	0.18
<i>Wildenowia striata</i> ² (Coastal Fynbos)	34.41	0.63*	3.92	1.06	58.01	2.6	0.06			0.15	1.10
<i>Pentzia incana</i> ² (Karrooid Broken Veld)	33.28	1.33*	8.27	6.83	45.82	5.8	0.20			0.62	0.19
<i>Mesembryanthemum</i> sp. ² (Karrooid Broken Veld)	19.22	1.22*	7.63	6.14	44.51	22.5	0.10			1.35	0.74
<i>Osteospermum sinuatum</i> ³ (Karrooid Broken Veld)	20.22	2.25*	14.01	3.37	40.36	22.04	0.20	>0.65	1.78	0.98	0.67

TABLE 6. (continued)

Species	Fe (ppm)	Cu (ppm)	Zn (ppm)	Mn (ppm)	Mo (ppm)	Co (ppm)	B (ppm)
<i>Protea cynaroides</i> ¹ (Mountain Fynbos)	37	2.7	4.5	95			11.8
<i>Wildenowia striata</i> ² (Coastal Fynbos)	68	4.4		37.4	0.40	0.09	
<i>Pentzia incana</i> ² (Karrooid Broken Veld)	820	18.8		103.0	0.61	0.50	
<i>Mesembryanthemum</i> sp. ² (Karrooid Broken Veld)	793	9.6		147.5	0.68	0.36	
<i>Osteospermum sinuatum</i> ³	186	6.2	41.7	172.2			

¹Vogts (1971), ²Stindt, Joubert (1979), ³Joubert, Stindt (1979)

*converted values

an area of Strandveld was about 50% but carrying capacity is low. Thus grazing 6 SSU ha⁻¹ for 14 days once a year and grazing 1 SSU ha⁻¹ for a 3 month period once a year both resulted in an approximately 25% decrease in canopy cover (Joubert, 1971). Less than one third of total plant cover is edible in Karrooid Broken Veld (Joubert, 1970). Carrying capacity is increased in some areas by reintroducing the indigenous palatable karoo plant *Osteospermum sinuatum* by overseeding in areas of Karrooid Broken Veld with disturbed soil surfaces (Joubert, van Breda, 1976). Renosterbosveld is generally considered quite unsuitable as a pasture. Selective grazing (often coupled with fire) results in an increase in cover of the unpalatable renoster-

bos (Levyns, 1956).

The carrying capacity of areas for successfully sustaining livestock have been determined for more arid parts of the Winter Rainfall Region through long-term successive approximation (Baard, 1978). Using carrying capacity as index of utilizable vegetation production, a significant trend emerges for such production to increase from the winter rainfall area through areas with rainfall throughout the year to areas with summer rainfall. This holds for more arid (Montagu - Colesberg transect) and more mesic (Montagu - Kirkwood transect) conditions (Fig. 1) but with a more rapid increase in utilizable production along the more mesic transect (Fig. 3). This tends to confirm a relatively lower

natural grazing potential in the area of winter rainfall as a whole.

Nutrient values of edible plant parts in natural vegetation of many veld types of the Winter Rainfall Region have been determined from several hundred different localities (Joubert et al., 1969; Stindt, Joubert, 1979; Joubert, Stindt, 1979). Composite samples consisted of all edible plant species pooled for a site. The mean nutrient values of plants for various veld types in July are given in Table 5. The fynbos and renosterbos types are essentially similar with respect to nutrient values both within and between types. This is despite the higher nutrient status soils of the renosterbosveld types relative to that of the fynbos veld types. Nutrient levels are generally low with phosphorous levels being deficient for animal nutrition throughout. The karroid types have a generally higher grazing quality potential than the fynbos or renosterbosveld types.

Chemical analysis of selected species, common in the given veld types, are listed in Table 6. The selected karroid species have generally higher nutrient levels than that of the fynbos species and the species Osteospermum sinuatum and Pentzia incana are not deficient in phosphorus. The succulent Mesembryanthemum has an exceptionally low fibre content and high ash content. The particularly low ash content in Wildenowia striata possibly reflects the leached nutrient deficient substrates associated with Cape Restionaceae. Leaf age affects nutrient levels. For example, in Protea cynaroides, phosphorous decreased with leaf age while calcium, magnesium, iron and manganese increased (Vogts, 1971).

4.3. Wild flower production

The commercial utilization of fynbos plants for ornamental purposes has expanded rapidly in the

last decade in the south-western Cape (Edwards, 1976). Plant categories used are mainly flower heads (for example, Protea), whole aboveground parts (for example, Erica), several "green" plants and seeds. Main reasons why several Protea species have assumed great importance as a source of cut flowers both for the local and export markets are: their unique beauty, being significantly different from practically all other flowers; their long lasting qualities as cut flowers; their suitability as cut flowers, having long stems; and their use in dried arrangements in the dead state (Rycroft, quoted Roux, 1979). Certain disadvantages have included sometimes rapid browning of leaves. In the year 1978/79 exports of fresh and dried proteas exceeded 2 million kg with the fresh flowers contributing more than two-thirds of the total (Roux, 1979).

Over 80% of current sales come from flowers picked in fynbos vegetation in the wild state (Edwards, 1976) with picking pressure on the vegetation appearing to peak around November (Roux, 1979). Pickers often cover areas to 1000 m up mountain slopes but difficulties of access often result in much damage and wastage (M.J. Wells, personal communication). There is an increasing tendency to prevent burning in picking areas which is very different to past practice and may affect plants that depend on fire. In some respects, natural field conditions are more favourable to Protea production. Natural fynbos conditions favour soil microbes that are antagonistic to Phytophthora cinnamomi which is commonly responsible for root rot in many Proteaceae under cultivation (Brits, von Broembsen, 1978). Root-knot nematodes also have a less unfavourable effect under field conditions (Rust, Myburgh, 1975). It appears that such factors tend to offset, to a certain extent, the advantages of irrigation and possible advantages of fertilization under conditions of cultivation. New work, however, is demonstrating economic advantages of grafting, cutting-propagation and

pruning in some fynbos species (Meynhardt, 1976). The growing utilization of selected ornamental elements of fynbos biomass of particularly the Mountain Fynbos areas may be expected to lead to more intensive management of this generally underutilized veld type in the future.

5. CONCLUSIONS

The data and findings presented tend to suggest more questions than answers to problems in identifying and understanding the determinants of plant biomass structural organization in the winter rainfall area of South Africa. There are particularly few data on the interaction between biomass structure and utilization patterns. Several unique features and the great complexity of the aboveground fynbos systems have been recognized, but research on the important belowground component is only just starting. Fynbos vegetation is not in isolation: it is closely intermeshed with many different vegetation types. Probably more than 50% of the area of Mountain Fynbos lies within 20 km of a semi-desert (karroid) margin. For answers to some of the research problems in fynbos, it may be necessary to also consider problems of adjacent vegetation types in the winter rainfall area. This may in turn help to resolve the question of possible irrelevance of winter rainfall - summer drought per se in determining the biomass structure of the vegetation. Future utilization patterns may be expected to result in rapidly increasing pressure being brought to bear on remaining fynbos vegetation. These pressures will need to be taken into account particularly in studying long-term functional patterns required for understanding current biomass structural patterns in the vegetation.

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THE EFFECTS OF FIRE INTENSITY, ASPECT AND SUBSTRATE ON POST-FIRE GROWTH OF CALIFORNIAN COASTAL SAGE SCRUB

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1. INTRODUCTION

The rapidity and nature of vegetative recovery after fire affects both long-term productivity and the potential for biomass utilization of Mediterranean-climate shrublands. While it has long been surmised that the pattern of post-fire succession is affected by the intensity of a burn in southern California shrublands (e.g. Keeley, 1977; Vogl, 1977), data are lacking on the thresholds of fire intensity above which particular shrub species will fail to resprout. Such information would be useful in predicting and managing the composition of shrublands under various fire frequency regimes. At the same time the effects of fire intensity are superimposed on those of other habitat factors in influencing the heterogeneous patterns of post-fire recovery in Californian shrublands.

We present here results from two field studies on patterns of post-fire recovery of summer-deciduous shrublands of southern California -- the coastal sage scrub or soft chaparral. The first study concerns regrowth of a coastal and two inland sites in which the pre-fire vegetative composition was measured, and the intensity of fire was calculated using a simulation model (FIREMODS; Albini, 1976) based on fuel load and weather conditions at the time of fire. The second study considers the recovery of three coastal sites of equal age, from a single locale, which vary in aspect or substrate, but which burned in a single fire whose intensity was similarly modeled. In both sets of observations, post-fire recovery has been followed over two growing seasons.

The results considered jointly provide a basis for understanding the relative importance of fire intensity in the post-fire succession of coastal sage scrub.

Coastal sage scrub occurs in the foothills of the Coast Ranges of Pacific North America, extending from San Francisco south to El Rosario in Baja California. The shrubland is dominated by mesophytic, malacophyllous shrubs, 0.5 - 2.0 m tall, and contains a largely ephemeral spring herbland flora. The type occurs on drier, often heavier-textured sites than the evergreen chaparral, and is generally found at lower elevations. On desert-margin sites, on the offshore islands, and at low elevations on the west coast of Baja California, the type becomes increasingly admixed with succulents (Mooney, 1977; Philbrick, Haller, 1977). Previous synecological accounts of the type include those of Kirkpatrick and Hutchinson (1977, 1980), Mooney (1977) and Westman (1980, 1981). Successional patterns in coastal sage scrub have been described by Westman (1980).

2. PROCEDURE

2.1. Study 1

Three 25 x 25 m stands of coastal sage scrub (Sites 1, 44 and 47) were sampled during 1977 and 1978 as part of a survey of 67 sites discussed elsewhere (Westman, 1980, 1981). At the time of initial sampling, the stands had not burned in 22, 21 and 20 years, respectively. Site 1 occurs 0.7 km from the coast, on a western-facing slope in the Santa Monica Mountains at Leo Carillo State Park, in northwestern

Los Angeles County. It was dominated before burning by typical coastal shrub species: Artemisia californica, Rhus laurina, Salvia leucophylla and Eriogonum cinereum. It burned at night on October 27, 1978, in a backfire set to check a large fire which burned 10,000 hectares in the Santa Monica Mountains.

Site 44 occurs 57 km inland, on a northeast slope just south of the City of Redlands in San Bernardino County. It was dominated by Encelia farinosa, a xeric species extending into portions of the Mohave and Colorado deserts. This site burned in an intense but localized fire in the late afternoon of July 22, 1978.

Site 47 is the most xeric of the three sites. It occurs 47 km inland, on an east southeast-facing slope on Double Butte at Homeland, near Hemet, in southeastern Riverside County. It was dominated by the narrow-leaved sclerophyllous shrub Eriogonum fasciculatum, and by the malacophyll, Artemisia californica. It burned in the early afternoon of June 18, 1978 in a localized fire which consumed several hectares on the lower slopes of Double Butte. When the upper slopes caught fire in June of the following year, a backfire was started which lightly burned portions of the scant herbaceous growth then extant on Site 47.

The pre-burn vegetation was sampled by recording foliar cover for each species intercepted by four randomly-placed 25 m line transects, and noting presence of additional species within the 0.063 ha site not intercepted by transects. While regrowth was still in the seedling and small resprout stage, post-burn sites were sampled by 20 one-meter square quadrats systematically placed along the original four transect lines. When vegetation regrowth was substantial enough (March 1979 for Site 1;

June 1979 for Site 47), further sampling was performed using line transects positioned as were those used on the pre-burn sample. Plant nomenclature follows Munz (1974). Soil was sampled at 15 cm depth from three random locations on the sites, before and after fire. Litter mass on the pre-burn sites was determined by weighing oven-dried litter from five randomly-placed 1/2 x 1 quadrats. Litter mass was corrected for the proportion of litter left on the ground at the end of collection (visual estimate). Sites 1 and 47 were sampled in December, March and June of 1979 and 1980; Site 44 was sampled in March and May, 1979 and 1980. To estimate fire intensity variables for the 1978 fires at these sites, FIREMODS (Albini, 1976) was obtained from the Lawrence Berkeley Laboratory computer center, University of California, Berkeley, and adapted to the University of California, Los Angeles computer system. Information used in the model is indicated in Table 1. In this model, fire intensity is derived primarily from the amount, fineness and moisture content of the fuel. A sensitivity analysis of the Rothermel model of fire spread, upon which FIREMODS is based in part, suggests that fire intensity is most strongly affected by fuel moisture content and quantity of dead fuel (Rothermel, 1972). A variable of some importance to fire intensity in both hard and soft chaparral is the volatile oil content of shrub species. The latter is reflected in the model only to the extent that seasonal changes in oil content affect heat contents of live fuel. Because such data were unavailable for sage scrub species, we used data on monthly changes in heat content of Adenostoma fasciculatum (chamise) (Philpot, 1969).

In presenting vegetational data, species richness is here defined as the number of vascular plant species per 0.0625 ha. Equitability using Whittaker's E_c index (Whittaker, 1972) is

Table 1. Data input for the fire intensity model (FIREMODS) of Albini (1976).

Site Characteristics	Study 1			Study 2			Source
	Site 1	Site 44	Site 47	South Slope Andesite	North Slope Sandstone	South Slope Sandstone	
Slope (degrees)	28	38	18	22	24	30	1
Aspect (degrees)	267	103	45	197	24	185	1
Air temperature at time of fire	16	36	36	31	31	31	2
Relative humidity at time of fire (%)	32	31	21	13	13	13	3
Time of fire	2:30AM	5:45PM	2:30PM	3:00PM	2:30PM	3:00PM	2
Fuel depth (m)	0.75	1.0	0.75	0.75	0.75	0.75	4
Fuel Characteristics							
Surface/volume ratio							
shrub foliage	1725	1725	1725	1725	1725	1725	5
branch (5 min, 0.16 cm diameter)	762	762	762	762	762	762	
branch (1 hr, 0.48 cm diameter)	254	254	254	254	254	254	
branch (10 hr, 1.59 cm diameter)	76	76	76	76	76	76	
branch (100 hr, 5.08 cm diameter)	24	24	24	24	24	24	
litter	940	940	940	940	940	940	
grass	3600	3600	3600	3600	3600	3600	
Fuel load (kg/m ²)							
Live							
shrub foliage	.195	.146	.249	.195	.195	.195	6
branch, 5 min	.073	.053	.092	.073	.073	.073	
branch, 1 hr	.219	.166	.278	.219	.219	.219	
branch, 10 hr	.610	.458	.776	.610	.610	.610	
branch, 100 hr	.073	.053	.092	.073	.073	.073	

Table 1. continued

Dead							
branch, 5 min	.019	.014	.024	.019	.019	.019	
branch, 1 hr	.053	.039	.068	.053	.053	.053	
branch, 10 hr	.146	.107	.185	.146	.146	.146	
branch, 100 hr	.019	.014	.024	.019	.019	.019	
litter	.617;1.55	.776	.214	.617	.617	.617	
grass	.053	.039	.068	.053	.053	.053	
Moisture content (fraction of dry weight)							
Live							
shrub foliage	.81	.91	.91	.81	.81	.81	7
branch, 5 min and 1 hr	.52	.58	.58	.52	.52	.52	
branch, 10 and 100 hr	.46	.52	.52	.46	.46	.46	
Dead	.06	.05	.03	.03	.03	.03	8
Moisture of extinction of dead fuel (fdw)	.20	.20	.20	.20	.20	.20	9
Heat of combustion (kcal/kg, (BTU/lb))							
Live							
shrub foliage	5554 (9999)	5277 (9500)	5277 (9500)	5554 (9999)	5554 (9999)	5554 (9999)	10
branches	5329 (9600)	5221 (9400)	5221 (9400)	5329 (9600)	5329 (9600)	5329 (9600)	
Dead	4444 (8000)	4444 (8000)	4444 (8000)	4444 (8000)	4444 (8000)	4444 (8000)	
Dry density of fuel (kg/m ³)							
Live							
shrub foliage	512	512	512	512	512	512	11
branches	736	736	736	736	736	736	

Table 1. continued

Dead							
branch, 5 min	769	769	769	769	769	769	
branch, 1 hr	777	777	777	777	777	777	
branch, 10 hr	785	785	785	785	785	785	
branch, 100 hr	793	793	793	793	793	793	
litter	778	778	778	778	778	778	
grass	769	769	769	769	769	769	
Total mineral content (fdw)							
shrub foliage and grass	.047	.047	.047	.047	.047	.047	12
branch, 5 min and 1 hr	.027	.027	.027	.027	.027	.027	
branch, 10 and 100 hr	.021	.021	.021	.021	.021	.021	
litter	.028	.028	.028	.028	.028	.028	
Silica-free mineral content (fdw)							
shrub foliage and grass	.035	.035	.035	.035	.035	.035	13
branches	.015	.015	.015	.015	.015	.015	
litter	.025	.025	.025	.025	.025	.025	

Notes to Table 1.

1. This study
2. Site 1: M. Sugarman, California Dept. Parks and Recreation, pers. comm.; Sites 44, 47: R. Licks, California Div. Forestry, pers. comm., Study 2 sites: Los Angeles Co. Fire Dept.
3. As in Note 2, except Site 1 value is estimated from Study 2 values, adjusted for temperature at Site 1.
4. This study. Site 1 values used for Study 2 sites.
5. Average values for shrub foliage and grass estimated from values in Countryman and Philpot (1970) and Albin (1976). For branches, values calculated for cylinders of diameters indicated. Time following branch size indicates response time to changes in atmospheric moisture.

Notes to Table 1. continued

6. Biomass of aboveground is partitioned into foliage (17%), live wood (67%), and dead wood (16%) based on the figures of J.T. Gray (pers. comm.; viz. Gray and Schlesinger 1980). The proportion of wood in each branch size category was computed using proportions for soft chaparral of 21-25 year age in Kessell and Cattelino (1978). Foliage was partitioned into shrub vs. grass using proportions of total foliar cover as grasses, measured in this study, as 21.9% (Site 1), 10.7% (Site 44), 44.9% (Site 47). The biomass of site 1 was taken as equal to that of the site of Gray and Schlesinger (1980), since the two sites are within c. 1 km of each other and were of the same age. The biomasses of Sites 44 and 47 were taken as the proportion the product of their canopy heights and foliage covers were to that of Site 1. For Site 1, the first litter mass value is from J.T. Gray (pers. comm.); the second, and the values for Sites 44 and 47 were measured directly. Study 2 sites were assumed to be identical to Site 1.
7. Values for moisture content of live foliage and wood are based on means for Salvia leucophylla, S. mellifera, and Artemisia californica during 16-22 July 1980, at the coast: foliage, 1.01 fdw; 5 min and 1 hr branches, 0.65 fdw; 10 hr and 100 hr branches 0.57 fdw. Adjustments for other months (Site 1, Study 2 and inland locations (Sites 44, 47) are estimated using moisture content in chaparral stands at 15 coastal and inland locations taken May-October 1979 (C.E. Conrad, pers. comm.), for Adenostoma fasciculatum in Los Padres National Forest, east of Santa Barbara, California (F. Cahill, pers. comm.), and data of Rothermel and Philpot (1973).
8. Dead fuel moisture (branches, litter, grass) estimated using U.S. Forest Service fuel moisture estimation procedure, adapted from the National Fire-Danger Rating system (Deeming et al. 1972). The procedure uses air temperature, relative humidity, slope percent, aspect, site exposure, month and time of day as input variables.
9. From figures for A. fasciculatum in Rothermel (1972) and Rothermel and Philpot (1973).
10. Live fuel figures from data for A. fasciculatum in Rothermel and Philpot (1973). Dead fuel figures from Albini (1976) and Nord and Countryman (1972)
11. Using A. fasciculatum, live foliage: Rothermel and Philpot (1973); live and dead branches: Countryman and Philpot (1970); litter: average of dead fuel.
12. Sum of values for ash, P, and K for A. fasciculatum of Countryman and Philpot (1970); litter is average of values.
13. Data for A. fasciculatum of Rothermel and Philpot (1973); litter is average of values.

calculated as $S/(\log n_1 - \log n_s)$ where S = total number of species, n_1 = cover of most dominant species; n_s = cover of least dominant species. Because cover values below 0.1% could not be measured accurately, 0.1% was the value assigned to species of this cover value or less. Simpson's index of concentration of dominance follows the format of Simpson (1949). Percentage similarity was computed using $PS = 2 \sum \min(n_a \text{ or } n_b)/(N_a + N_b)$ where n_a , n_b are cover values of a given species in Sites A or B, and N_a , N_b are the sum of cover value in Sites A and B, respectively (Czekanowski, 1909). Coefficient of community was $CC = 2S_{a,b}/(S_a + S_b)$ where S_a , S_b are the number of species in Sites A and B, respectively, and $S_{a,b}$ is the number of species common to both sites (Sørensen, 1948).

2.2. Study 2

The three 25 x 25 m stands of coastal sage scrub in the second study are within 0.5 - 2.4 km of the coast, and are to be found within a 4.8 km stretch of dissected coastline in the western Santa Monica Mountains, near Site 1 of Study 1. The sites differ mainly in aspect and substrate. An east northeast-facing sandstone site was located on a slope adjacent to lower Zuma Canyon, and a southwest-facing andesite site was located near Trancas Canyon. Vegetation on all three sites was 22 years old, and the three sites burned in the same fire at about 2:30 pm on October 26, 1978. The wind was blowing from the north at 50-90 km/hr. Since age of the sites is identical to that of the coastal site (Site 1) of Study 1, and post-fire vegetation quite similar to that of Site 1, pre-burn fuel load characteristics for the Study 2 sites were taken as identical to Site 1. Fire intensities for the three sites of Study 2 were therefore virtually identical.

Post-burn vegetation sampling was accomplished by estimating percent foliar cover in 50 1 x 1 m quadrats arrayed along two 25 m belt transects. As in Study 1, additional species present on the site were assigned an arbitrary cover value (0.1%). Post-fire soil samples were collected from 0-15 cm depth at four locations within each site. Indices used in the analysis of floristic data are the same as those of Study 1.

3. RESULTS

3.1. Study 1

3.1.1. Habitat features of the sites. Table 2 provides data on community structure before the fires, topographic features, climatic and soil features, including mineral nutrient analyses at 15 cm depth before and after fire, and impact factors. Potential evapotranspiration is plotted in Figure 1. The xeric natures of Site 44 and 47 are reflected in Figure 1 by their high potential evapotranspiration rates, and in Table 2 by their lower moisture-holding capacities relative to Site 1. The lower litter mass at Site 47 is possibly a result of the light, periodic grazing to which the site is subjected. Soil analyses indicate the enrichment of all three sites, especially with N, P and K, following release of these nutrients from vegetation by fire. Absolute levels of mineral elements are higher at Site 1 after the fire than at the other two sites, presumably because of higher initial biomass.

3.1.2. Fire intensity and post-fire reproductive patterns. Fire "intensity" is represented in Table 3 by "reaction intensity", which is the rate of heat release per unit area of ground at the fire front. A second datum of relevance is the range of windspeeds during the fire since, with more rapidly-moving fires, the duration of heat at a point will be less, and the maximum temperature reached at a point

Table 2. Community structure and habitat variables for the three sites of Study 1.

	Site 1	Site 44	Site 47
<u>Community structure before fire</u>			
Litter mass, g/m ²	1552	775	216
Average canopy height, m	0.75	1.0	0.75
Maximum canopy height, m	1.75	2.0	1.75
% light penetration to 10 cm height	49	65	38
<u>Topography and position</u>			
Latitude	34°03'08"	34°01'36"	33°43'52"
Longitude	118°56'04"	117°12'27"	117°05'15"
Distance from coast, km	0.68	73.9	57.3
Elevation, m	46	442	575
Slope, degrees	28	38	18
Aspect, degrees	267 (W)	103 (ESE)	45 (NE)
<u>Climate</u>			
Mean annual precipitation, cm	36	32	27
Mean maximum temperature, warmest month, °C	24	36	38
Mean minimum temperature, coldest month, °C	7	3	1
<u>Soils</u>			
Bulk density, 8 cm depth, g/cm ³	1.56	1.50	1.60
Substrate	shale	sandstone	graywacke shale partly metamorphosed to schist
Texture	loamy fine sand	loam	fine sandy loam

Table 2, cont.

	Site 1		Site 44		Site 47	
	pre- burn ¹	post- burn ²	pre- burn ³	post- burn ⁴	pre- burn ⁵	post- burn ⁶
Soil, 15 cm depth						
% water, half saturation	25	28	20	18	16	28
pH	6.6	6.9	7.2	8.0	6.4	6.1
Salinity (EC x 1000)	0.3	0.5	0.4	0.4	0.2	0.9
Nitrate, ppm	6	44	14	21	10	28
Ammonium, ppm	2	46	1	9	2	26
Phosphate-P, base-extractable (NaHCO ₃), ppm	4	43	11	14	5	21
Potassium, ppm	73	401	103	169	106	353
Calcium, ppm	4140	4420	2410	3380	730	950
Magnesium, ppm	990	1300	150	126	185	161
Total nitrogen, ppm	2100	2620	1300	619	800	1670
1)6-20-77, 2)12-10-79, 3)7-22-77 4)7-4-80 5)3-28-78 6) 12-10-79						
<u>Impact factors</u>						
Grazing	none		none		periodic, light	
Fire date, most recent	10-27-78		7-22-78		6-18-78 and 6-14-79	
Date of previous fire	1956		1957		1958	

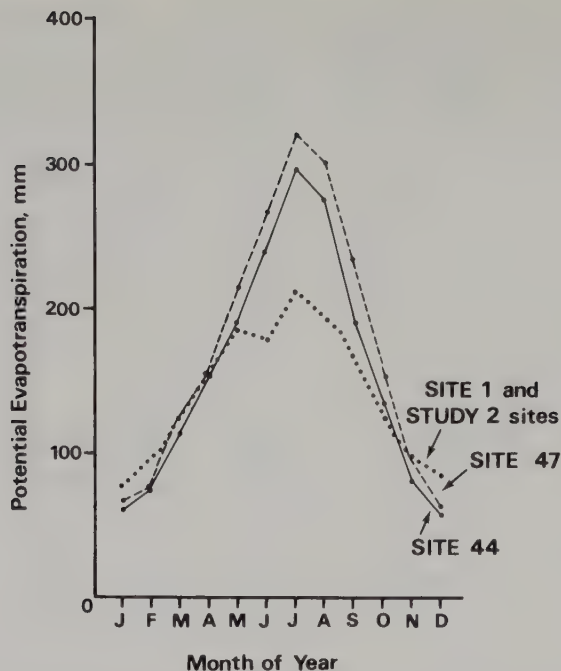


FIGURE 1. Monthly potential evapotranspiration, mm, calculated by the method of Christiansen (1968). Values for Site 44 are taken from Norton Air Force Base, 8 km north. Values for Site 47 are taken from March Air Force Base, 15 km NNW. Values for Site 1 and the sites of Study 2 are averages between the Oxnard and Los Angeles International Airports, which are approximately 45 km NW and 42 km SE of the sites, respectively.

greater, assuming total fuel combustion. In terms of ultimate effect on root structures, these two fire attributes act counter to each other, and it is impossible to say from the present model what the effect of differing windspeeds would be on subsurface heat exposures. A number of soil properties affect the rate of transfer of heat from ground surface to the surface of roots. Of these, soil moisture is most important (DeBano et al., 1977), but soil texture and mineralogy are also influential. Biological attributes such as rooting depth and physiological tolerances of root tissue to heat will also influence the extent of damage to root systems, and factors such as root crown size and the post-fire growing environment will influence the vigor of regrowth.

From Table 3 it can be seen that fire intensity was equal or greater at the coastal site (Site 1) of Study 1, than at the two inland sites. Two litter mass values were used to estimate fire intensity at Site 1. Using the lesser value, the fire intensity of Site 1 is comparable to that of Site 44, and both are 1.5-fold greater than the intensity of Site 47. Using the greater litter mass value, the fire intensity at Site 1 exceeds that of the two inland sites. Figure 2 illustrates the residual heat release from the burning or smoldering of dead fuel following the passage of the fire front, calculated from Subroutine BURNOUT (Albini, 1976). Sites 1, 44 and the Study 2 sites experienced a relatively rapid burnout of dead fuel at relatively high reaction intensities (one minute exposures to 32 - 40 kcal

Table 3. Fire characteristics at the six sites of Studies 1 and 2, as estimated by the computer simulation model, FIREMODS (Albini, 1976).

	Site 1 (1)	(2)	Site 44	Site 47	S-slope andesite	N-slope sandstone	S-slope sandstone
Reaction intensity, windspeed 0 km/hr, kcal sec ⁻¹ m	370	170	170	120	200	200	200
Windspeed at time of fire, km/hr	0-2	0-2	10-15	10-15	50-90	50-90	50-90
Total heat released by dead fuel which burned after passage of fire front, kcal m		3170	3660	1420	3230	3230	3230
Predicted duration of fire in absence of wind, min		3.0	2.2	3.8	2.6	2.6	2.6
% contribution to reaction							
Dead fuel	77	58	72	38	62	62	62
Live fuel	23	42	28	62	38	38	38

(1) Using litter mass values measured at Site 1 (1560 g m^{-2}). (2) Using litter mass value (617 g m^{-2}) measured by Gray and Schlesinger (1980) at a site c. 1 km inland from Site 1. (3) To convert to $\text{BTU/min}^{-1}/\text{sq. ft.}^{-1}$, divide by 0.04521. (4) Windspeeds for Site 44, Norton Air Force Base; Site 47, March Air Force Base; remaining site data sources in Note 2, Table 1. (5) To convert to BTU/sq. ft. , divide by 2.713.

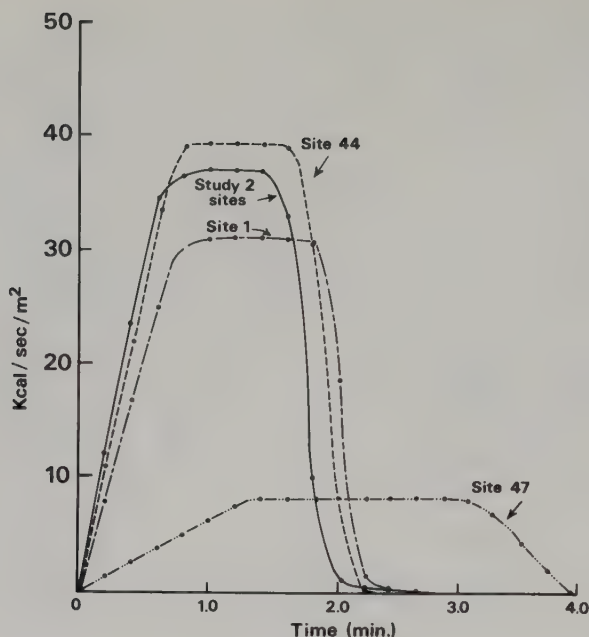


FIGURE 2. Rate of heat release (reaction intensity) from dead fuels after the passage of the igniting flame front, sites of Study 1 and 2. To convert from $\text{kcal sec}^{-1} \text{sq. m}^{-1}$ to $\text{BTU min}^{-1} \text{sq. ft.}^{-1}$, divide by 0.04521.

$\text{sec}^{-1} \text{m}^{-2}$), whereas Site 47 experienced a cooler but longer burnout (2 minute exposure to $9 \text{ kcal sec}^{-1} \text{m}^{-2}$). Because the longer duration of heat and the lower heat input at Site 47 are counterbalancing in direction of effect, it is not possible to say what differential effect the distinct nature of the burnout curve for Site 47 would have on root structures. The total heat released during this burnout period was similar for Sites 1, 44 and Study 2 sites, and about 40% of this amount at Site 47 (Table 3).

On the basis of field observations of vegetative recovery, by contrast, Site 1 experienced a much more rapid recovery than Sites 44 and 47, ascribable primarily to the vigor of

crown sprouting from shrub dominants at Site 1. All eight shrub species present at Site 1 before fire resprouted vigorously (Table 4 and Appendix I). By contrast, no shrub species resprouted at Site 47, and only a few scattered individuals resprouted at Site 44. *Artemisia californica* was present at all three sites before fire, but resprouted with some regularity only at Site 1, produced one resprouting individual at Site 44, and none at Site 47. *Mirabilis californica* was present at Sites 1 and 44, but resprouted only at Site 1. A single individual of *Encelia farinosa* resprouted at Site 44, and not until the second growing season; *Eriogonum fasciculatum* did not resprout at all at Site 47, but a minority did resprout on Study 2 sites. By contrast the

Table 4. Shrub species of coastal sage scrub which resprout following fire, based on field observations on 18 sites in southern California and Baja California. The maximum fire reaction intensity in $\text{kcal sec}^{-1} \text{m}^{-2}$ ($\div 0.04521 = \text{BTU min}^{-1} \text{ft.}^{-2}$) above which root crowns fail to resprout is estimated based on results from Studies 1 and 2. Species which resprouted at Site 1 are asterisked. ¹These species appear better able to withstand intense fires at the coast than inland.

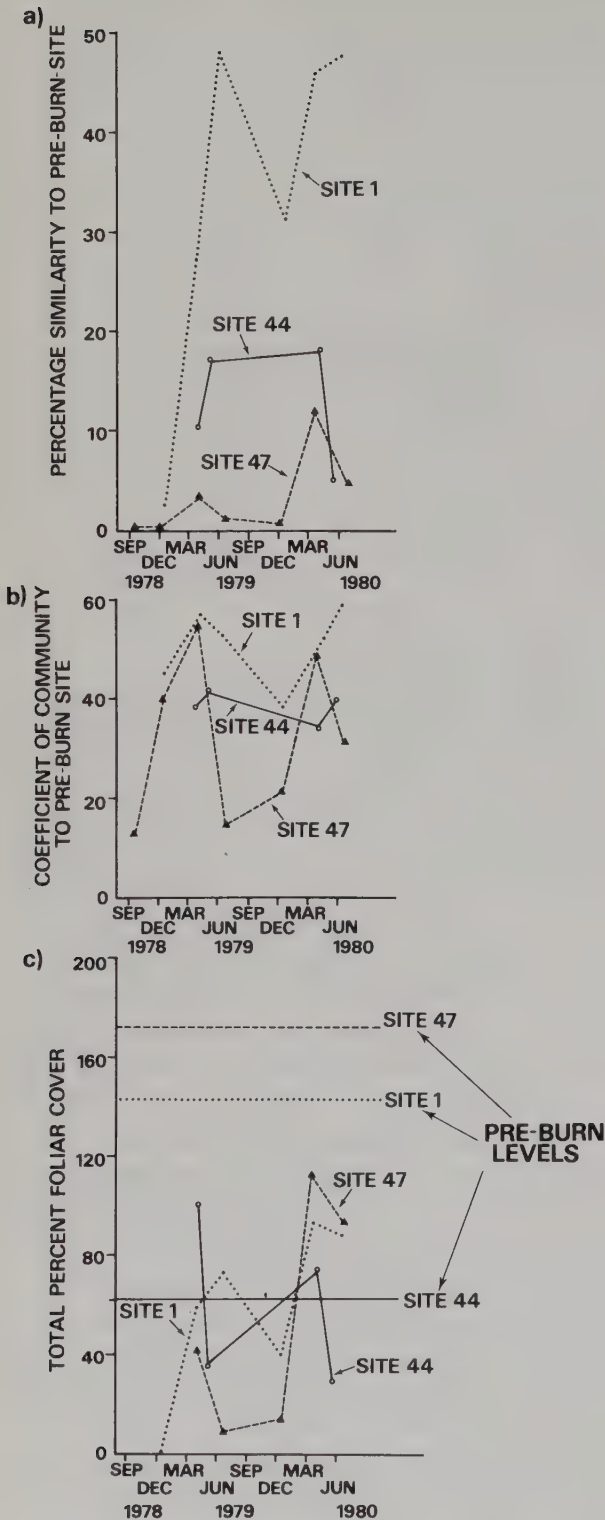
From belowground organs		From belowground organs	
<u>Acalypha californica</u>		<u>Rhus integrifolia</u>	(>200)
<u>Artemisia californica</u>	(>200)	<u>Rhus laurina</u>	(>200)
<u>Corethrogyne filaginifolia</u>	(>200)	<u>Rhus ovata</u>	(>200)
<u>Encelia californica</u> *	(>200)	<u>Salvia apiana</u>	(<120)
<u>Encelia farinosa</u>	(<170)	<u>Salvia leucophylla</u> *	(>200)
<u>Ephedra californica</u>		<u>Salvia mellifera</u> *	(>200)
<u>Eriogonum cinereum</u> *	(>200)	<u>Sambucus mexicana</u>	(>120)
<u>Eriogonum fasciculatum</u>	(<120 to >200) ¹	<u>Simmondsia chinensis</u>	
<u>Euphorbia misera</u>		<u>Yucca schidigera</u>	(>170)
<u>Haplopappus squarrosus</u>	(>200)	<u>Yucca whipplei</u> *	(>200)
<u>Keckiella cordifolia</u>	(>200)		
<u>Marah macrocarpus</u>	(<120 to >200) ¹	From aboveground organs	
<u>Mimulus longiflorus</u>	(>200)	<u>Artemisia californica</u> *	
<u>Mirabilis californica</u> *	(>200)	<u>Eriogonum cinereum</u> *	
<u>Opuntia littoralis</u>	(>200)	<u>Eriogonum fasciculatum</u>	
<u>Opuntia parryi</u>	(>170)	<u>Franseria chenopodifolia</u>	
<u>Rhamnus crocea</u> *	(>170)	<u>Keckiella antirrhinoides</u>	
<u>Rhamnus ilicifolia</u>	(>200)	<u>Salvia apiana</u>	
<u>Rhus diversiloba</u>	(>200)	<u>Vigueria laciniata</u>	

congeners Eriogonum cinereum and Encelia californica at the coast (Site 1) resprouted vigorously by the first growing season. On the basis of these results and those of Study 2, some initial estimates of fire tolerance of shrub species are compiled in Table 4.

By the end of the second year following the burn, the coastal site (Site 1) had approached the pre-burn floristic composition qualitatively by 59%, compared to 40% and 30% for Sites 44 and 47, and quantitatively by 48%, compared to 5% for Sites 44 and 47 (Figure 3). These results may be attributed largely to reestablishment of individuals by crown sprouting at Site 1.

The existence of resprouted individuals, however, also enhanced reproduction by seedlings of these species on the site. All shrub species which resprouted were observed to flower and set seed in the first year following fire. By June or December, 1979, seedlings were observed at Site 1 which had not been observed earlier in the growing season (e.g. Eriogonum cinereum, Artemisia californica, Encelia californica, Yucca whipplei). This implies that the seeds of the species did not survive the soil temperatures during fire, or that seed dormancy does not occur beyond one season in these species. An abundance of seedlings of Encelia californica was observed immediately downslope of a resprouted individual of this species in

FIGURE 3. a) Percentage similarity of Study 1 sites to pre-burn vegetation. b) Coefficient of community between post- and pre-burn vegetation of Study 1 sites. c) Total foliar cover, %, on Study 1 sites. Horizontal lines mark total cover of pre-burn sites.



March, 1980. Seedlings of this species had first appeared in December, 1979, but were scant. These observations suggest that, at least for *Encelia californica*, sources of seed for reproduction come largely from resprouted individuals which set seed in the first year, and not significantly from long-range dispersal.

Since *Encelia* seeds (Asteraceae) are relatively light and windborne, this "self-sowing" mechanism may be even more important for heavier-seeded species of low heat tolerance. Especially following extensive fires, such species would otherwise be selected against in the central portion of the burned area. The virtual failure of shrub species to crown sprout on the inland sites (44, 47) may thus have further retarded site recovery by failing to provide an *in situ* seed source for subsequent seedling reproduction.

Rosettes of *Yucca whipplei* which crown sprouted and fruited in the first season following fire died following fruiting. New rosettes sprouted from the base of the dead ones. Presumably flowering in subsequent rosettes will not occur for some years, as is normal for this species. Hence this species exhibits a "dual-pulse" strategy of reproduction. Seeds are produced in the first year following fire, aiding reestablishment of the population. Subsequent seed loads are released only after the species has accumulated starch reserves over several years. The seeds from this second crop are more likely to find suitable sites for colonization following long-range dispersal.

3.1.3. Recovery of floristic composition. In Figure 3 total cover values for the three sites show spring peaks, as do CC and PS indices. In the case of Site 44, cover values already exceeded pre-burn levels. Pre-burn sampling was performed on this site on July 22, after spring ephemerals had died. Cover values in the spring of 1979 and 1980 may not have exceeded pre-burn levels had pre-burn data for springtime been available from this site. It is noteworthy that similarity of post- to pre-burn vegetation at Site 1 continues to increase in late spring, while it declines by this time at inland sites. This observation may be ascribed to at least two factors. Firstly, the more moderate coastal climate and lower potential evapotranspiration (Figure 1) allows persistence of understorey grasses and herbs later in the growing season. Secondly, the similarity of the coastal site to its pre-burn condition is due more to its shrub composition than is the case at the inland sites. Consequently, composition does not change as dramatically in late spring when grasses and forbs die off.

3.1.4. Diversity. In Figure 4, aspects of species diversity at the three sites before and after fire are plotted. The high richness and equitability, and low concentration of dominance, in the spring (March) sample intervals reflect the post-fire herb flora which characterizes this community type (Westman, 1980) and which is also observed in hard chaparral (e.g. Hanes, 1977). Westman (1980) has reported on the subsequent decline in richness and equitability that occurs as the stand ages over a 40 year period. The elevated richness and equitability of all three sites following fire tells us nothing of the "recovery" of the sites in terms of their likelihood to proceed in a succession to a steady-state resembling the pre-burn pyric climax. In fact, data from Figure 3 demon-

strated the large differences in recovery of floristic composition to pre-burn levels between sites. These observations may serve to emphasize the inappropriateness of using diversity indices alone in tracking post-impact recovery of chaparral ecosystems.

Figure 4 plots the rate of appearance of new species to the sites. It is interesting to note that for Sites 1 and 47, after the spring bloom the rate of addition of new species dropped off exponentially, consistent with the shape of immigration curves of new species to islands proposed by McArthur and Wilson (1967). The reason for the appearance of a significant number (ten) of new herb species in the second spring at the desert-margin site (Site 44) is unknown and may simply be due to chance factors of dispersal.

There is a tendency for equitability of all sites to be high due to the presence of a relatively large number of herb species which do not persist as shrub cover develops (Westman, 1980). There is some tendency for the evenness of resource distribution among herb species to be higher, however, at the coast. At inland sites, naturalized Mediterranean grasses (*Bromus rubens*, at Site 44, *Avena barbata* at Site 47) or forbs (*Erodium cicutarium*, Site 47) attain strong dominance in the herb cover.

3.2. Study 2

In the three sites of the second study, fire reaction intensity, distance from coast, elevation, air pollution, climate and age of stand before fire are held constant (Table 5); aspect and substrate vary. While the small number of sites prevents the calculation of standard errors, certain broad trends appear evident in the patterns of recovery.

3.2.1. Recovery of floristic composition. Figure 5 suggests that aspect is a more influential

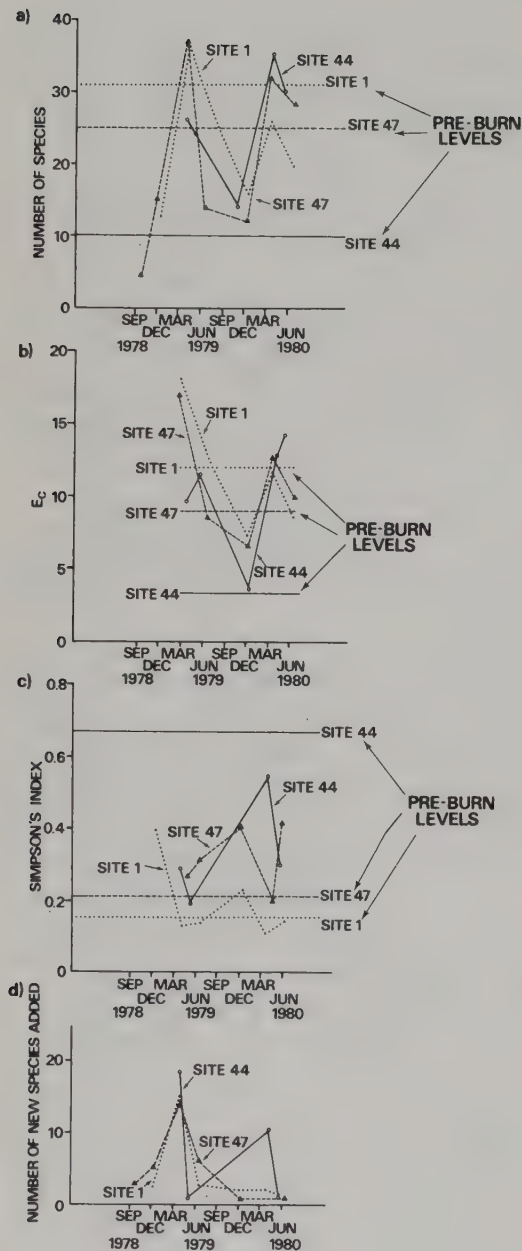


FIGURE 4. Diversity of Study 1 sites compared to pre-burn condition (horizontal lines). a) Species richness. b) Equitability, Whittaker's E_c . c) Concentration of dominance, Simpson's index. d) Number of new species added.

variable in affecting composition, both qualitatively and quantitatively, than is a contrast in substrate between volcanic (andesite) and sedimentary (sandstone). Sites of differing aspects are the least similar floristically, and do not become more similar in the second year. There appears to be a compensatory effect between aspect and substrate, however, with south-facing andesite sites being more similar to north-facing sandstone sites than sandstone or S-facing sites are to each other. Possible explanations for this result include (a) the higher moisture-holding capacity of andesite at wilting point (Table 5). In the early part of the growing season, this additional moisture retention may compensate for the higher evaporative stress to which the S-facing slope is exposed, perhaps resulting in a water budget comparable to N-facing sandstone. (b) The more comparable pH, cation exchange capacity, soil calcium and phosphorus between these particular andesite and N-facing sandstone sites may help induce the similarities in vegetation. Kirkpatrick and Hutchinson (1980) and Westman (1981) have shown the importance of certain substrate variables in affecting coastal sage composition. Nitrogen is regarded as the most influential element from these studies, however, and it is impossible to evaluate the significance of the soil nutrient differences from the few data available presently.

The dominant shrubs returning to the three sites following fire were similar to those of the coastal site (Site 1) of Study 1 (Appendix I). *Encelia californica* and *Salvia mellifera* were among returning shrubs on the two S-facing sites. *Eriogonum cinereum* was important on both sand-

Table 5. Habitat variables for the three sites of Study 2, Santa Monica Mountains

	S-facing sandstone	S-facing andesite	N-facing sandstone
<u>Topography and position</u>			
Latitude	34°2'30"N	34°2'00"N	34°2'00"N
Longitude	118°49'00"W	118°49'50"W	118°52'20"W
Distance from coast, km	2.4	1.0	0.5
Elevation, m	110	120	120
Slope, degrees	30°	22°	24°
Aspect, degrees	185°(S)	197°(SW)	35°(ENE)
<u>Climate</u>			
Mean annual precipitation, cm	36	36	36
Mean maximum temperature, warmest month, °C	24	24	24
Mean minimum temperature, coldest month, °C	7	7	7
<u>Soils, post-burn</u>			
Texture	loam	loam	silt loam
Water, % of saturation at 1/3 atm	17	25	21
pH	6.9	5.5	5.6
Salinity (EC X 1000)	0.9	1.1	0.4
Phosphate-P, base-extractable (NaHCO ₃), ppm	26	7.7	6.9
Potassium, ppm	274	352	117
Calcium, ppm	4629	2766	2505
Magnesium, ppm	620	778	717
Total nitrogen, ppm	2000	2500	2500
Sulfate, ppm	<1	44	7
Cation exchange capacity, meq/100 g	24.7	21.6	21.6

Table 5, continued

	S-facing sandstone	S-facing andesite	N-facing sandstone
<u>Impact factors</u>			
Grazing	none	none	none
Fire date, most recent	10-26-78	10-26-78	10-26-78
Date of previous fire	1956	1956	1956

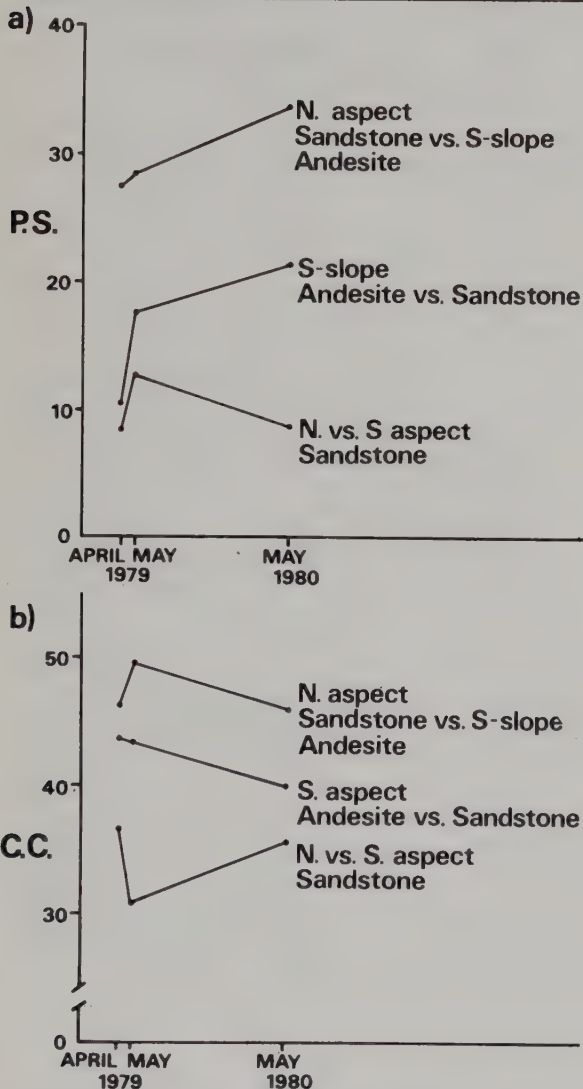


FIGURE 5. Comparison of floristic composition between sites of Study 2. a) Percentage similarity. b) Coefficient of community.

stone sites, and *Haplopappus squarrosus* and *Salvia leucophylla* on the andesite and N-facing sandstone sites. Two species, *Eriogonum fasciculatum* and *Marah macrocarpus*, resprouted on the Study 2 sites, while failing to resprout on Site 47 which had been estimated to have a lower fire reaction intensity. Whether this anomaly is due to an error in the estimation of fire intensity, or to ecotypic differences among coastal and inland populations of these widespread and highly variable species, cannot be determined at present.

3.2.2. Diversity. Figure 6 indicates that the S-facing andesite slope is the richest in species, and the most equitable. It exceeds in these regards all other sites in both Studies 1 and 2. At the same time, this site has the lowest total cover value (Figure 6d), suggesting that lack of rapid recovery by shrub species is here responsible for the maintenance of a rich herb flora. The same phenomenon was observed for Site 44 in Study 1, and in a previous study of succession on coastal sites of sage scrub (Westman, 1980).

The range of variation in diversity variables is on the whole smaller for the sites of Study 2 than for those of Study 1, suggesting that substrate and aspect are somewhat less influential on diversity than fire intensity, distance from coast, or other parameters which varied among sites of the first study. The trend towards a slight decline in richness and equitability by the second year, reflected by these sites,

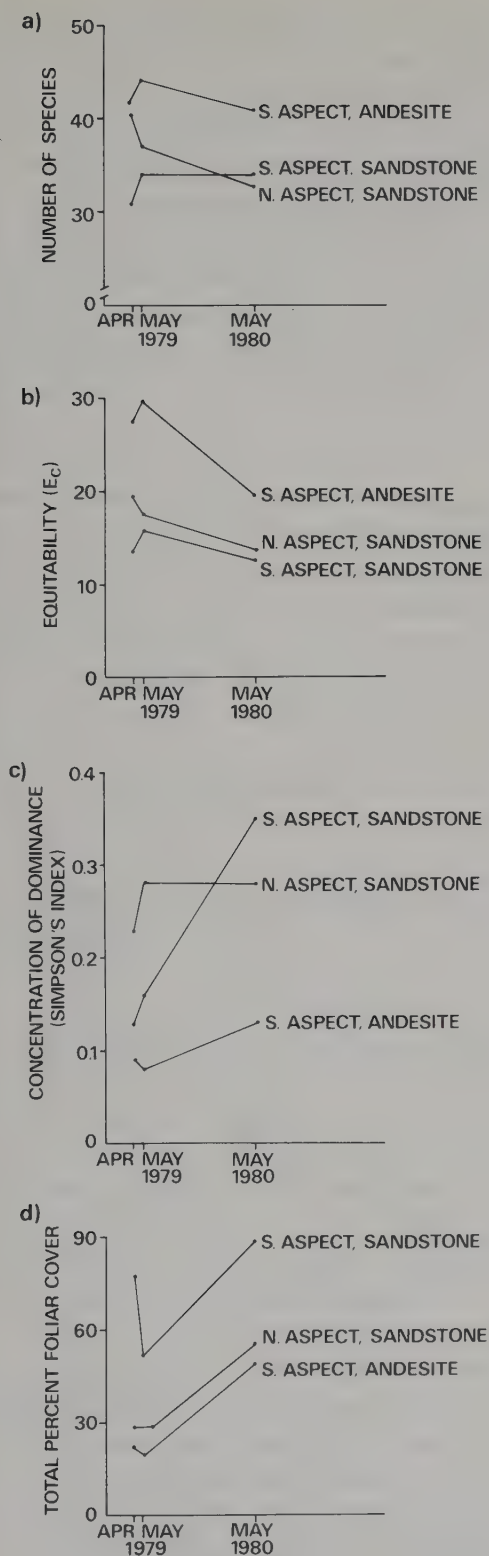


FIGURE 6. Diversity of Study 2 sites. a) Species richness. b) Equitability, Whittaker's E_c . c) Concentration of dominance, Simpson's C index. d) Total percent foliar cover.

and by Sites 1 and 47, in the first study, are consistent with the expected long-term decline in the values of these variables (Westman, 1980).

4. DISCUSSION

4.1. Role of fire intensity in post-fire recovery

The coastal sites (Site 1 of Study 1, Study 2 sites) exhibited a markedly greater degree of crown sprouting and hence floristic recovery than the inland sites (Sites 44, 47), despite experiencing fires of equal or greater intensity than the inland sites according to computer model predictions. Several hypotheses to explain these results are plausible. (1) Estimates from the fire model may not reflect accurately the actual fire intensity which occurred at the sites. (2) The belowground parts of species at the coastal site may have higher tolerances to intense fires, or may more commonly have intrinsic crown-sprouting ability, than the species present at the inland sites. (3) Post-fire growing conditions may have been less favorable at the inland sites. Evidence for and against each hypothesis will be examined in turn.

4.1.1. Accuracy of model predictions. Field observations had suggested to us that Sites 1 and 44 had experienced less intense fires than Site 47, since short stem stubs survived and resprouted after the fire at Sites 1 and 44, whereas no plant parts remained aboveground after the fire at Site 47. Among model input parameters which may have contributed to misestimation of fire intensity, the value for litter mass is perhaps most suspect. Litter mass values are difficult to measure accurately due to the high degree of spatial heterogeneity in litter distribution. By using the value for litter mass at a site similar to Site 1 but c. 1 km further inland (Gray, Schlesinger, 1980) which was only 40% as great, the reaction intensity at Site 1 was reduced to

47% of the value originally estimated. This suggests that the relationship between litter mass and reaction intensity is practically linear in this instance. The revised estimate for fire intensity at Site 1, however, is still 1.5-fold greater than the intensity of Site 47, so that if inaccuracy of model predictions are to be blamed, other misestimations among data inputs, or unrealistic assumptions of the model would have to have occurred.

4.1.2. Sensitivity of species to fire intensity and intrinsic crown-sprouting ability. The species dominants at the three sites are different. At Site 1, the species which contributed the most cover by resprouting were, in decreasing order, Eriogonum cinereum, Salvia leucophylla, Encelia californica and Yucca whipplei. At Site 47, the major dominants before fire were Eriogonum fasciculatum and Artemisia californica. Artemisia californica was also present before fire at Site 1, and was not a vigorous resprouter at that site, suggesting either that its innate resprouting capacity or its tolerance to heat, is low. Eriogonum fasciculatum, while having vigorous capacity to sprout from aboveground parts, is not a vigorous sprouter from belowground parts, perhaps because the species does not have a well developed root crown. About 20% of the individuals of E. fasciculatum observed on Study 2 sites were resprouting from belowground parts, the remainder being seedlings. The failure of E. fasciculatum to resprout at all at Site 47, despite a lower estimated fire reaction intensity than at coastal sites, is initially puzzling if reaction intensity estimates are accepted as reliable. It may be, however, that there are ecotypic differences between coastal and inland populations of the species. Tratz and Vogel (1977) failed to observe sprouting from belowground parts of E. fasciculatum

at a desert site of northern San Diego County in which resprouting of many other shrub species was observed. The high genetic variability in the species is attested by the formal recognition of four subspecies by Munz (1974). Thus while the possibility of misestimation of fire intensities cannot be ruled out, the lack of rapid recovery at Site 47 can also be explained by the presence on the site of more fire-sensitive species or ecotypes, and obligate seeders, in the first instance.

At Site 44, the dominant shrub before fire was Encelia farinosa. This species reproduced almost exclusively by seed. Only one individual was seen which was apparently arising as a crown sprout. Hence, as on Site 47, the dominant pre-burn species were either highly intolerant of heat exposure, or had poor intrinsic abilities to resprout from root crowns.

It is interesting to speculate that inland sites in general contain fewer sprouting species because of less frequent fires, but in fact lightning-initiated fires tend to be more frequent inland (Keeley, 1977) in this region. Many more replicates of this study are needed before generalizations can be proffered on this point.

4.1.3. Unfavorable post-fire growing conditions inland. The possibility exists that some features of the physical environment were less favorable to plant growth on inland sites than Site 1 in the first growing season following fire. An examination of Table 1 indicates that topographic features were, if anything, more favorable on Site 47 (less steep, NE rather than W aspect). Soil nutrients, especially N-P-K, were 2 - 3 - fold higher on Site 1, so that soil fertility cannot be ruled out as a factor enhancing recovery on Site 1. All soil nutrient levels are above pre-burn levels, however, so that differences are likely to affect only the vigor of sprouts, and not the capacity to resprout. The rainfall

during the growing season of 1978-79 was unusually high at all three sites, being highest at Site 47. The rainfall incident upon the three sites from the time of fire in 1978 to end of March 1979, and departure from average for this period was as follows: Site 1 49 cm (departure, +10 cm); Site 47, 87 cm (+60 cm); Site 44, 45 cm (+17 cm). Rainfall cannot therefore be considered as a factor discouraging crown sprouting at inland sites during the 1978-79 growing season.

In sum, while errors in modeling of fire intensity cannot be ruled out, the poorer recovery of vegetation on the two inland sites compared to Site 1 can also be explained on the basis of the presence of more obligate seeders and fire-tolerant species or ecotypes on the inland sites. The lower soil fertility levels on inland sites may have hindered growth rates relative to the coast, but are unlikely to have prevented the appearance of resprouts altogether.

4.2. Relative roles of fire intensity, aspect and substrate

The differences in pace and manner of recovery of Site 1 relative to Sites 44 and 47 will be a function in part of habitat growing conditions. Study 2 suggested the favorableness of southerly aspects, and to a lesser extent andesitic substrates, to recovery as measured by foliar regrowth. It must be recognized, however, that these results are correlative only, that sample sizes are small, and that other habitat factors remain uncontrolled.

An examination of post-fire recovery performance compared with aspect or substrate in Study 1 (Table 2 and Figures 3, 4) shows that neither aspect nor substrate type is a consistent predictor of the observed degree of recovery of the sites. The stark differences

in resprouting on sites which differed in fire intensity, compared with the less variable results on sites differing only in aspect or substrate (Study 2) and less consistent results using aspect and substrate as predictors in Study 1, suggest that fire intensity is a more important factor influencing post-fire vegetative recovery than aspect or substrate. Fire intensity alone, however, cannot be taken as a simple guide to post-fire recovery; predictions must be based on a knowledge of the crown-sprouting ability of the pre-burn vegetation, and the heat-tolerance of underground organs of the dominant species. Among the variables of aspect and substrate in Study 2, aspect appeared the more influential variable when other factors were controlled, but the need to replicate these experiments with much larger sample sizes, and better control of covariable factors, is obvious.

4.3. Resilience

It is of interest to examine what can be learned from these studies about the "resilience" of coastal sage scrub to fire impact. The term ecosystem "resilience" has been used to refer to the pace and manner of recovery of an ecosystem following perturbation (Westman, 1978). As such, several components of resilience can be recognized. "Amplitude" refers to the threshold beyond which an ecosystem will fail to recover its original steady-state (Orians, 1975; Westman, 1978). We are unable to conclude whether any of the sites in this study will eventually recover 80 - 100% of their percentage similarity to the pre-burn condition because two years is insufficient for such recovery to be demonstrated. It was noted, however, that Site 1 far exceeded Sites 44 and 47 in its recovery to the pre-burn condition by the second year, based on floristic composition (CC 59% vs. 40 - 36%; PS 48% vs. 5%). Significantly, the dominant shrubs had reestablished their positions of dominance on Site 1 by the end of two years, and had reappeared scarcely

or not at all on Sites 44 and 47. This suggests that the "amplitude" of Sites 44 and 47 had been exceeded.

A second feature of ecosystem "resilience" is the pace of recovery, termed "elasticity" (Orians, 1975; Westman, 1978). Site 1 is exhibiting higher elasticity than Sites 44 or 47. Indeed it is possible that, despite their later starts, Sites 44 and 47 will eventually recover their pre-burn compositions in the absence of fire, in which case the amplitude of these sites will not have been exceeded. To quantify either of these components would require a lengthier sample period. Westman (1978) has suggested that the time required to achieve 50% PS with the original steady state would be a useful standardized measure of elasticity. In the present study, the coastal site reached this level within two years, while the inland sites had only reached a tenth of this level within two years. This result emphasizes that elasticity is a property not of the ecosystem alone, but one which is affected as well by the degree of stress applied.

The elasticity of these sage scrub sites may be compared with the elasticity exhibited by a dry heath on sand dunes of southeast Queensland, Australia which had been cleared during surface mining. The rate of recovery by the heath is slower, even when topsoil is returned, and the soil is fertilized and stabilized. After two years, CC to a vegetation resembling the pre-mine state was 15% (Westman and Rogers, 1977).

Because the three sites in the first study were not identical in species and habitat composition to begin with, it must be recognized that abilities to recover from a fire of identical intensity might differ. In this

case we would be able to observe something of the differences in "malleability" (Westman, 1978) of the three communities, defined as the extent to which the new steady-states differ from the original when systems are exposed to identical perturbations.

It would be of interest to expose patches of vegetation of similar composition and habitat to fires of different (and known) intensities, but it would not be easy to accomplish this in practice without introducing some other variables (time of day or year of fire; age of stand) simply to achieve differences in fire intensity. In the field study of phenomena at the ecosystem level, the existence of multifactored experimental situations, and the framing of conclusions in probabilistic terms, seems inevitable.

4.4. Concluding remarks

To predict, and ultimately to manage, a stand of coastal sage for biomass utilization, honey production, fire hazard reduction or other purpose, we must know more about the response of sage scrub dominants to high soil temperatures and post-fire growing conditions. Nevertheless, there is now more strongly suggestive evidence that fire intensity may be one of the variables inducing the mosaic pattern of associations that can be seen on landscapes covered with coastal sage scrub. It seems equally clear that the periodicity of prescribed burning, or the effective fire frequency resulting from fire exclusion or other policies, will affect fire intensity and hence vegetative composition. These effects in turn will influence significantly the success of any long-term management plan for California shrublands and their analogues.

5. SUMMARY

The hypothesis that fire intensity significantly affects post-fire vegetative recovery patterns in summer-deciduous shrublands is examined. Fire

intensity was quantified on three sites of Californian coastal sage scrub whose pre-burn vegetative compositions were known, and post-fire vegetative recovery was observed over two years. Fire intensities could effectively explain the differences in post-fire vegetative recovery only after apparent differences in the intrinsic crown-sprouting abilities and belowground heat tolerances of dominant species present before fire were taken into account. A coastal site populated by crown-sprouting species of high tolerance to heat exhibited a percentage similarity of 50% to the pre-burn vegetation within two growing seasons, following a fire of moderate intensity. By contrast, two inland sites burned by fires of comparable or lower intensity resembled their former compositions by only 5% after two years. This result was ascribed primarily to the relative lack of crown-sprouters and heat-tolerant species among the pre-burn dominants. In a second study, recovery was observed on three sites at one locality which burned in a single fire of approximately uniform intensity. Sites differing in aspect (north vs. south-facing) were more profoundly different in the nature of returning vegetation two years after fire than were sites which differed in substrate (volcanic vs. sedimentary). In examining results of the two studies jointly, it appears that fire intensity can affect post-fire composition more profoundly than can aspect or substrate differences. These results suggest ways in which fire management policies affect both vegetative composition and the potential for biomass utilization in Californian summer-deciduous shrublands.

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Appendix I. Percent foliar cover values for species at the three sites of Study 1, before burning, and in the spring of the second growing season after fire.

* indicates species present at another sample period after fire.

	Site 1		Site 44		Site 47	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
Date of sampling	6-20-77	3-20-80	7-22-77	4-5-80	3-28-78	3-21-80
<u>Artemisia californica</u>	33.6	2.6		0.1	20.7	0.1
<u>Amsinckia intermedia</u>						0.1
<u>Apiastrum angustifolium</u>		0.4				
<u>Avena barbata</u>	1.5	1.9		0.1	0.3	32.7
<u>Bebbia juncea</u>			0.1			
<u>Brassica nigra</u>	0.1	0.1	0.1	6.8		0.1
<u>Bromus diandrus</u>	0.1				0.9	
<u>Bromus mollis</u>		*				*
<u>Bromus rubens</u>	4.0	15.6	6.8	54.2	44.1	5.3
<u>Calandrinia ciliata</u>					0.1	4.7
<u>Calochortus catalinae</u>	0.1	*				
<u>Calochortus splendens</u>						*
<u>Calystegia macrostegia</u>		5.2		5.2		0.1
<u>Camissonia californica</u>				0.4		
<u>Camissonia intermedia</u>				*		
<u>Camissonia micrantha</u>	0.1					
<u>Castilleja affinis</u>	0.1					
<u>Centauria melitensis</u>		0.1				
<u>Claytonia perfoliata</u>					0.1	2.1
<u>Conyza bonariensis</u>						*
<u>Conyza canadensis</u>				0.1		

	Site 1		Site 44		Site 47	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
<u>Crassula erecta</u>				0.1	2.2	1.0
<u>Croton californica</u>				0.1		
<u>Cryptantha intermedia</u>	0.1		0.1			*
<u>Daucus pusillus</u>	0.1				1.8	*
<u>Delphinium parryi</u>					0.1	*
<u>Dichelostema pulchella</u>	0.1	0.7		0.1	2.6	0.2
<u>Dudleya lanceolata</u>				0.1		
<u>Elymus condensatus</u>		*				
<u>Emmenanthe penduliflora</u>		*		*		0.2
<u>Encelia californica</u>	2.4	9.5				
<u>Encelia farinosa</u>			50.6	0.2		
<u>Eremocarpus setigerus</u>						*
<u>Eriogonum cinereum</u>	14.7	13.2				
<u>Eriogonum fasciculatum</u>			0.7	0.1	54.2	
<u>Eriogonum gracile</u>						*
<u>Eriophyllum confertiflorum</u>		*				0.1
<u>Erodium cicutarium</u>	0.1	0.1		1.3	0.5	27.6
<u>Erodium moschatum</u>						0.3
<u>Escholzia californica</u>		0.1				
<u>Eucrypta chrysanthemifolia</u>				0.1	0.2	0.1
<u>Festuca myuros</u>						25.3
<u>Festuca octoflora</u>					30.9	0.5
<u>Filago arizonica</u>						*
<u>Filago californica</u>		*				0.1
<u>Galium angustifolium</u>	0.3	0.1				

	Site 1		Site 44		Site 47	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
<u>Galium nuttallii</u>		0.1				
<u>Gilia capitata</u>						0.5
<u>Gnaphalium californicum</u>						0.1
<u>Gnaphalium microcephalum</u>		0.1				
<u>Hypochaeris glabra</u>		0.1				0.1
<u>Isomeris arborea</u>		1.1				
<u>Jepsonia parryi</u>					0.1	0.3
<u>Keckiella antirrhinoides</u>				0.1		
<u>Lactuca serriola</u>						*
<u>Lamarckia aurea</u>		*				
<u>Lasthenia chrysostoma</u>						0.1
<u>Lepidium virginicum</u>					0.1	*
<u>Lolium multiflorum</u>				0.1		
<u>Lotus salsuginosus</u>	0.1	*		0.6		0.1
<u>Lotus scoparius</u>	0.1	7.2				0.5
<u>Lupinus bicolor</u>		*				0.3
<u>Lupinus densiflorus</u>				0.1		
<u>Lupinus hirsutissimus</u>		*				
<u>Lupinus sparsiflorus</u>	0.1			0.1		
<u>Lupinus succulentus</u>		*				
<u>Malacothamnus fasciculatus</u>				0.1		
<u>Malacothrix saxatile</u>		*		0.1		
<u>Marah macrocarpus</u>		0.8		0.1	0.1	*
<u>Melica imperfecta</u>	0.1					
<u>Mentzelia micrantha</u>		*				

	Site 1		Site 44		Site 47	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
<u>Mimulus pilosus</u>						*
<u>Mirabilis californicus</u>	0.1	2.4	1.4	3.1		
<u>Muhlenbergia microsperma</u>				0.1		
<u>Nemophila menziesii</u>	0.1				0.6	1.0
<u>Opuntia littoralis</u>	0.1					
<u>Opuntia parryi</u>			2.1	0.1		
<u>Oxalis albicans</u>	0.1					
<u>Pellaea mucronata</u>					0.3	
<u>Phacelia cicutaria</u>		*				0.1
<u>Phacelia distans</u>				0.1		
<u>Phacelia minor</u>				0.3		
<u>Phacelia parryi</u>		0.1				
<u>Pityrogramma triangularis</u>					0.1	
<u>Plagiobothrys tenellus</u>					1.4	1.1
<u>Platystemon californicus</u>						*
<u>Pterostegia drymarioides</u>					0.7	
<u>Rafinesquia californica</u>				*		
<u>Rhamnus crocea</u>	0.1	0.1				
<u>Rhus integrifolia</u>	4.2					
<u>Rhus laurina</u>	22.4	0.2				
<u>Salvia apiana</u>					1.7	
<u>Salvia columbarae</u>				0.2		
<u>Salvia leucophylla</u>	21.4	11.6				
<u>Salvia mellifera</u>	1.5	*				
<u>Schismus barbatus</u>				0.8	1.5	*

	Site 1		Site 44		Site 47	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
<u>Senecio vulgaris</u>				0.1		
<u>Silene gallica</u>	0.1					
<u>Solanum parishii</u>				0.1		
<u>Sonchus oleraceus</u>		0.1		0.1		0.5
<u>Stephanomeria virgata</u>		*				*
<u>Stillingia linearifolia</u>			1.7	0.3		
<u>Stipa lepida</u>	29.0	11.7				
<u>Tetradymia spinosa</u>						0.5
<u>Trifolium tridentata</u>						*
<u>Tropidocarpum gracile</u>					0.1	
<u>Yucca schidigera</u>			0.1	0.1		
<u>Yucca whipplei</u>	6.8	8.5				
Bare ground		23.3		28.6		15.5

PRODUCERS AND THE FIRE CYCLE IN A PHRYGANIC ECOSYSTEM

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1. INTRODUCTION

The severe summer drought combined with high temperatures leads to a high frequency of fires in mediterranean-type ecosystems. The relation of this climatic type with fire has been long ago noted (Griesebach, 1872). Shantz (1947) refers to the mediterranean-type ecosystems of California as "fire-type" or "fire-climax". The numerous adaptations of plants dominating mediterranean-type ecosystems indicate that fire has been a strong selective force and that these systems can be considered as "fire-induced" or "fire-adapted" (Jepson, 1930; Naveh, 1973; Biswell, 1974).

According to Mutch (1970) ecosystems subject to frequent fires over evolutionary time have developed characteristics, which make them extremely flammable. This point of view is reinforced by the fact that these ecosystems have developed adaptations which result in their surviving fire and further periodic fires of about every 15 years or so, appear necessary to maintain their maximum diversity and productivity* without frequent fires, fuels would accumulate in high quantities, and then fires would lead to large changes in ecosystem structure (Biswell, 1974).

According to Naveh (1975) adaptations to fire can be considered as an homeostatic feedback control. Positive feedback responses are those which result in overcoming the after-effects of fire by increased physiological activity. This is chiefly expressed by vegetative resprouting, fire-stimulated seed germination and post-fire flower and seed production. Negative feedback responses can be regarded as all those mechanisms which enable the avoidance of the fire hazard, either by direct tolerance of seeds or plant organs, or by their reduced physiological activity during critical fire periods.

Le Houerou (1973) reviewing the effect of fire

on mediterranean vegetation types, classified them as either active or passive pyrophytes according to their positive or negative feedback responses. Phrygana species (plants of the arid mediterranean-climate regions of Greece) seem to be active pyrophytes. They have developed, in the course of evolution, several features that make them very flammable. Their leaves are small, hairy and have thin cuticles. They have slender shoots with fine loosely arranged twigs, while most of the dead shoots remain on the mature plants. On the other hand, the dead leaves which fall at the base of the plants during the summer period provide a substrate for quick spreading fires. Two major types of plant regeneration can be distinguished: obligatory resprouters (mainly maquis), which regenerate vegetatively from undisturbed underground buds and facultative resprouters (mainly phrygana) which in addition can regenerate by seeds. Vegetative regeneration in obligate resprouters begins almost immediately after fire, but is delayed in facultative ones until the first rains. This difference has been attributed to the different depths reached by the root systems of the two plant groups (Naveh, 1975).

Fires are very frequent in the phrygana communities. This study reports on part of multifaceted eco-physiological study designed to provide information about Greek phryganic ecosystems and especially fire's effect on them.

2. SITE DESCRIPTION

A phryganic ecosystem located at Mount Hymettus, near Athens University Campus was studied. It was burnt accidentally in July 1976 (Fig. 1).

3. METHODS

Throughout a two years period, burnt and control sites were frequent surveyed. Seedlings of woody plants dominating the ecosystem were counted in ten $1m^2$ plots randomly selected in the burnt site.



FIGURE 1. Aspect of the burned and unburned site

At the same study site the total aboveground vegetation was cropped monthly by means of 10 randomly-spaced 1m line intercepts. Ground litter (all dead organic material on the ground down to the surface of the mineral soil) was also collected from the same plots. The samples were oven-dried and weighed. From these data total and relative percentage biomass as well as litter present were calculated. Measurements were also taken of the heights of the dominant woody plants. In addition their leaf size and chlorophyll content were determined.

4. RESULTS AND DISCUSSION

Seed germination after fire in the phryganic ecosystem is very characteristic in the case of *Cistus* spp. (Arianoutsou-Faraggitaki, Margaritis in press). Under normal conditions, germination occurring in autumn is about 10 to 20 seedlings per square meter, while after fire it rises dramatically to 300-400 seedlings per square meter

(Fig. 2). Similar data are noted by Papanastasis (1977) for *Cistus salvifolius* and *Cistus monspeliensis*, as well as for other regions (Le Houerou, 1973; Naveh, 1974). *Cistus* species have been considered by all these investigators as obligatory seed regenerators (Naveh, 1975; Papanastasis, 1977; Arianoutsou-Faraggitaki, Margaritis, in press). Most of the dominant phryganic species are facultative resprouters. Forty-five days after fire the burned plants of *Sarcopoterium spinosum* produce new leaves from their root crowns. One month later *Euphorbia acanthothamnus* and *Phlomis fruticosa* develop resprouts in the same way. The new leaves of these resprouts are soft, large and with intense green colour (Fig 3).

Even though the resprouting begins in a period in which all the leaves of the unburnt plants are small (summer leaves, Margaritis, Papadogianni, 1978) the new leaves of the resprouted species are larger. This difference in leaf size exists during almost all the first post-fire year (Fig. 4).

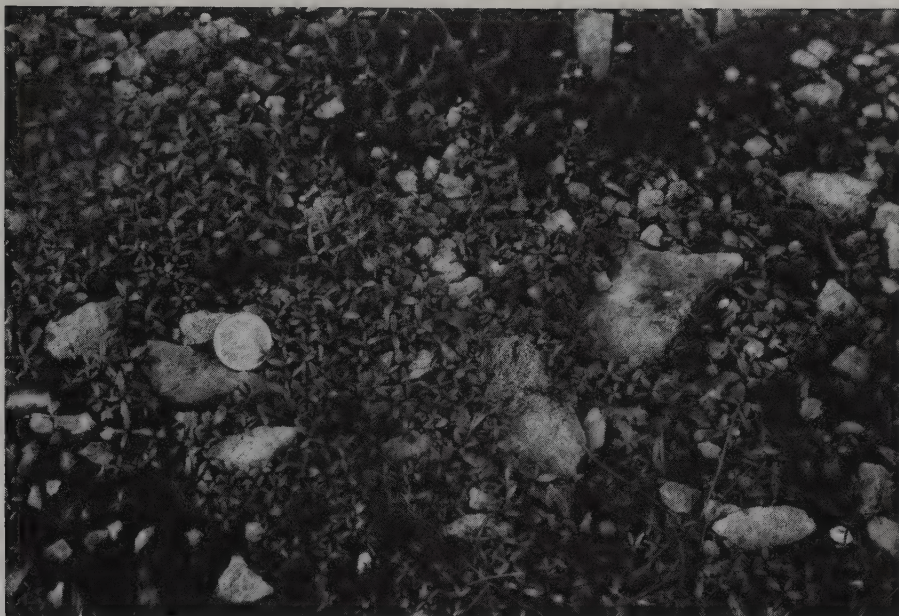


FIGURE 2. Cistus spp seedlings in the burned site



FIGURE 3. Comparison between Phlomis fruticosa resprouted and unburned plants

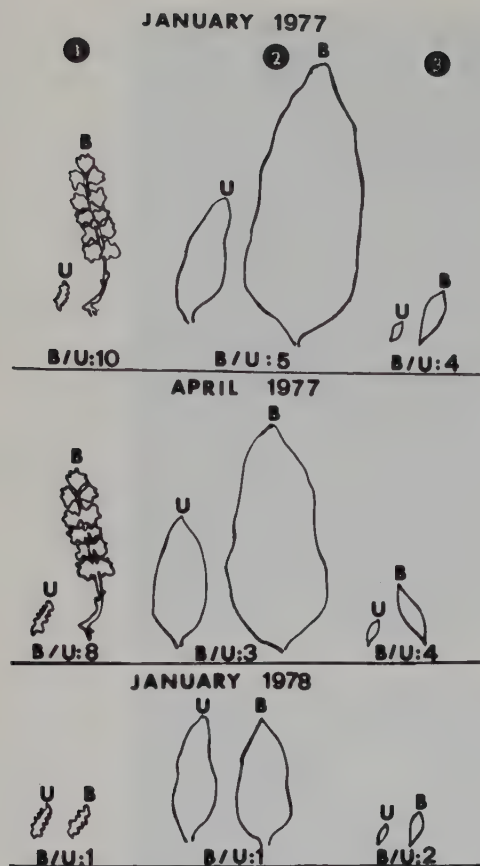


FIGURE 4. Comparison between resprouted and unburnt plant leaf sizes in *S. spinosum*, *P. fruticosa* and *E. acanthothamnos*

In a period of nine months after the fire the resprouts reach a level of maturity so that they have gradually developed the characteristics of seasonal dimorphism (new, smaller leaves, spiny formations, woody shoots) and are thus adapted for the unfavourable drought conditions of the summer (Fig. 5).

During the first post-fire year, *E. acanthothamnos* and *S. spinosum* form flowers and fruits, while *P. fruticosa* flourishes the second post-fire year, a fact that in normal conditions does not happen until the fourth or fifth year (Fig. 6)

Phenological differences between resprouted and unburnt plants during the second post-fire year

are not great. The leaves of the resprouted are still larger, but smaller than those of the previous year. The resprouting woody species of *P. fruticosa*, *E. acanthothamnos* and *S. spinosum* attain almost their original height by the end of the study period (Fig. 7).

Naveh (1973) indicates that *S. spinosum* reaches 40 cm high within two years after fire, while Papanastasis (1977) stated that phrygana sprouts, in general, attain one third of their original height by the end of the first growing season. Parsons (1976) found that *Adenostoma fasciculatum* (chamise chaparral of California) was about 40-60 cm tall 4 years after fire. Papanastasis (1977) notes that, in general, phrygana plants produce seeds by the second season after fire.

Unfortunately, there are no data available regarding plant phenology after fire in mediterranean-type ecosystems. Data on the midwestern American grasslands (Kucera, Ehrenreich, 1962; Hadley, Kieckhefer, 1960) refers to a significant acceleration in the life cycle of the dominant species, which was attributed to such factors as: 1) litter removal, 2) earlier growth of species as a result of the higher soil temperature after burning, 3) greater quantities of available nutrients and 4) greater radiation.

Probably, the same processes would also operate in the phrygantic ecosystem. As mentioned above, mediterranean-type ecosystems are fire-induced and fire-adapted. So, they possess an endogenous rhythm which determines their numerous adaptations but with a general feature: the quick response to environmental conditions, especially fire. Otherwise, all those characteristics would have ceased acting as adaptations. The new leaves of the resprouting plants are not only larger, but richer in chlorophyll than normal. No doubt, photosynthesis is also significantly increased (Table 1).

The herbaceous vegetation which usually grows among the woody phrygantic species are also adapted to recurrent fires. Many workers have noted the scarcity of herbs in mature mediterranean-type ecosystems (Sampson, 1944; Went et al., 1952; Horton, Kraebel, 1955; McPherson, Muller, 1967, 1969; Chou, Muller,



FIGURE 5. Seasonal dimorphism on *P. fruticosa* leaves (summer and winter leaves)

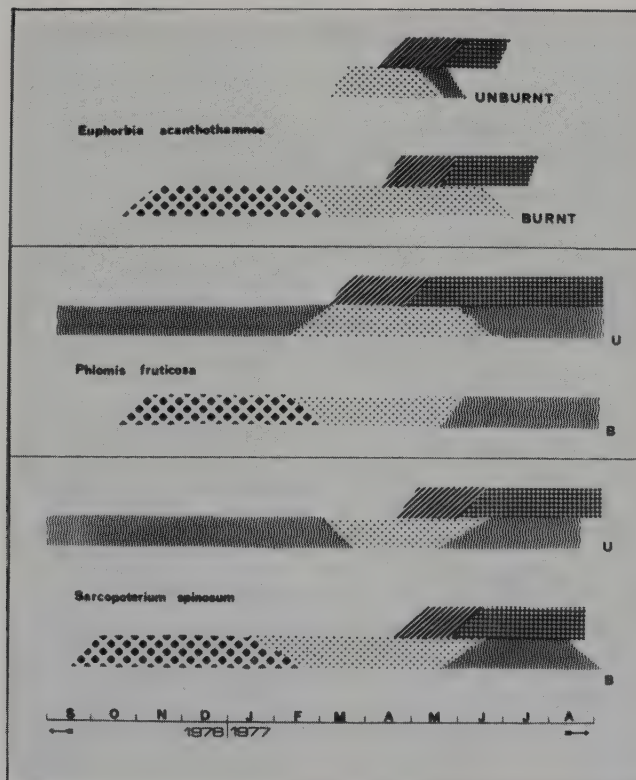


FIGURE 6. Phenological stages of the resprouting species during the first post-fire year

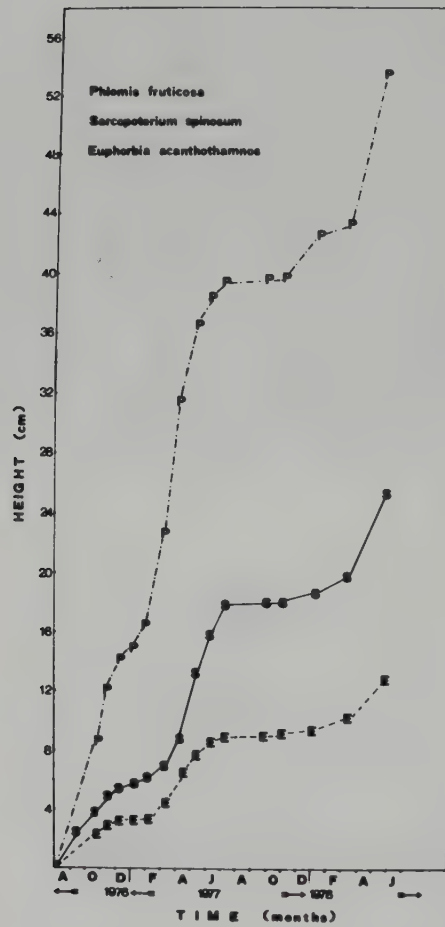


FIGURE 7. Growth in height of the resprouting species, during the study period

TABLE 1. Total chlorophyll content

	Total chlorophyll (mg.g ⁻¹ leaf dry weight)		
	Phlomis fruticosa	Sarcopoterium spinosum	Euphorbia acanthothamnos
JANUARY 1977			
Unburnt plants	2.0	2.3	4.7
Burnt plants	3.5	5.7	5.4
Increase %	70	150	17
APRIL 1977			
Unburnt plants	2.4	2.2	4.9
Burnt plants	4.6	5.0	5.2
Increase %	90	128	7
JANUARY 1978			
Unburnt plants	4.0	3.6	6.3
Burnt plants	3.2	4.4	8.6
Increase %	-18	17	36

1972; Christensen, Muller, 1975). After fire, however, such areas are often carpeted with annual and perennial herbaceous species rarely seen in the undisturbed sites. The seeds of many of these herb species lie dormant in the soil beneath the shrubs from one fire to the next. The numbers of seedlings are highest in the first and second years following fire (Naveh, 1974). Germination is restricted and the herb population gradually diminishes as the shrub cover increase. The temporal dominance of herbs and their subsequent decline in our study site is shown in Figure 8. In the phryganic ecosystem, typical examples of post-fire herbs are Andropogon hirtus, Asphodelus microcarpus, many species of Cyclamen, Allium, Ornithogallum, Arisarum vulgare, Crocus nudifolius and the Papilionaceae, especially Trifolium spp., Lathyrus aphaca, Medicago spp., Lotus spp., Vicia spp., etc. The presence of the latter has been correlated with nitrogen replenishment after

fire in the site, since as much as 96% of site nitrogen can be lost in the smoke of a fire (Arianoutsou-Faraggitaki, Margaris, in press). Probably the abundance of herbs in burnt areas may be related to one or more of the following causes: 1) removal of the shrub cover and litter, 2) inactivation of phytotoxic materials produced by the shrubs, 3) more available nutrients in the soil, 4) decreased competition with the shrubs, for a short at least period (Sweeney, 1967; Muller et al., 1968 etc).

On April 1975 the relative percentages of P. fruticosa, E. acanthothamnos, S. spinosum and Cistus spp., in the total aboveground biomass were 33%, 24%, 13% and 8% respectively, while that of the other woody plants and herbs (Helianthemum sp., Thymus capitatus, Asparagus aphyllous) was 22% (Margaris, 1976). After fire and in the same growth season (April 1977) the situation was quite different: the relative percentages of P. fruticosa, E. acanthothamnos, S. spinosum and Cistus spp., were 5%, 3%, 3% and 5% respec-

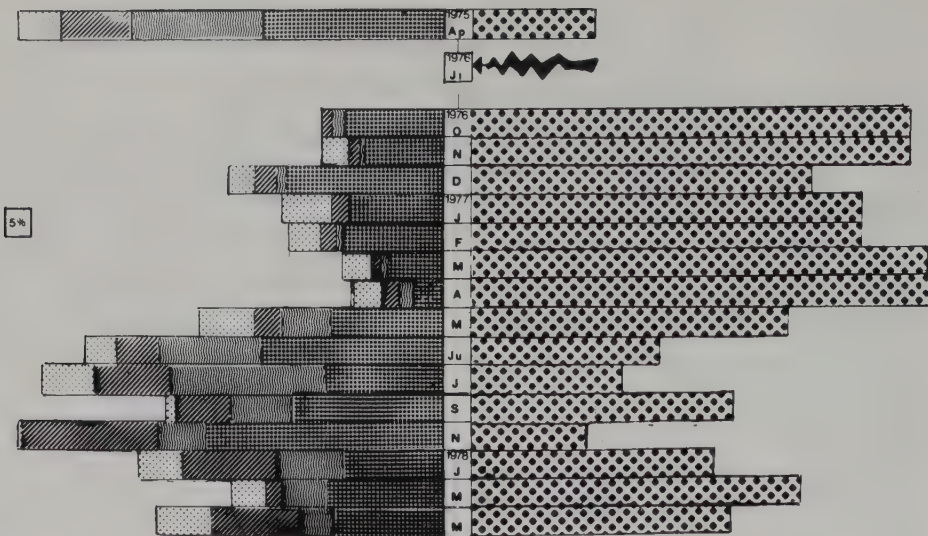


FIGURE 8. Relative biomass percentages

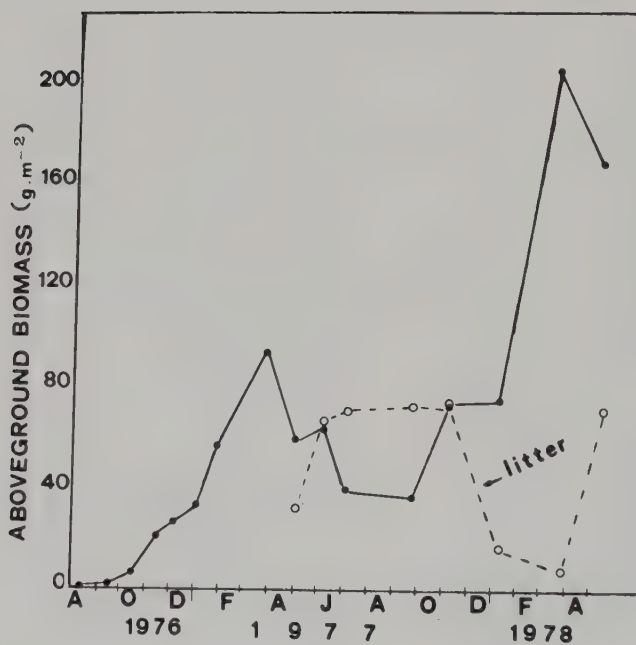


FIGURE 9. Total aboveground plant biomass measured during the study period.

tively, while for all the rest (mainly herbs) together, was 83%. It is therefore, quite obvious how the growth of the herbaceous vegetation increased. This situation lasts for the autumn and winter months till early spring. By the end of spring and the beginning of the summer the herbs dry out. The following growing season the situation is not the same but is still different from the prefire one. The secondary succession is not a series of plant substitutions but rather a gradual increase in dominance of perennial species which were found in the stand before fire. This process has been formed autosuccession (Hanes, 1971).

The changes in total plant biomass with time are plotted in Figure 9. Biomass production on April 1977 was 8% of the prefire production (1,111 g. m⁻², Margaris, 1976) while the following year (April, 1978) it was 19%, which means that an increase of 55% in biomass production took place. At the end of the study period the total biomass was about 200 g.m⁻².

Papanastasis (1976) found that standing biomass in a Phlomis fruticosa community was 3,000 kg. ha⁻¹; on the other hand, in S. spinosum community it was 1,200 kg.ha⁻¹ in the second and 2,800 kg. ha⁻¹ in the third year after fire.

Sampson (1944) found that at the end of the first growing period Adenostoma fasciculatum resprouts were 173.5 g.m⁻². Within 8 years it became 1,279 g.m⁻², growing at a mean rate of 110 g.m⁻².year⁻¹, recovering 40% of the original productivity. Long et al. (1967) and Specht (1969) noted that in the first 10 post-fire years of autosuccession the annual productivity of sclerophylls in France, California and W. Australia was 150g.m⁻².

Considering the above data and noting that from the first to the second year the biomass increase in the phryganic ecosystem was about 100 g.m⁻² we can assume that within 5-10 years full reconstitution would take place.

5. CONCLUSIONS

Fire, either natural or man caused, has been part of the Greek environment for thousands of years (Liakos, 1973). Phryganic ecosystems are adapted to fire and depend on them for their continued maintenance. As Papanastasis stated (1976) Phlomis fruticosa and Sarcopoterium spinosum plants would not live longer than 20-30 years unless they were burned and hence revitalized.

Our results are in agreement with those found in analogous mediterranean ecosystems of the world (Italy, Spain, Israel, Chile, Australia, S. Africa and USA): The lack of water in combination with the high summer temperatures lead to fire in the phrygana. This ecosystem type covers quickly by resprouting and/or activation of seed germination. This rapid recovery is probably in part due to the high photosynthesis rate of young leaves of resprouts.

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PRODUCTIVITY AND NUTRITIONAL RESPONSES OF CHAMAEBATIA FOLIOLOSA (ROSACEAE) TO SEASONAL BURNING

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1. INTRODUCTION

An important area for research in Mediterranean-type ecosystems is the relationship of seasonal burning to patterns of productivity and nutrient uptake in evergreen shrublands subject to regular environmental fires. The broad importance of fire as an ecosystem factor and specifically with regard to its impact on nutrient cycling processes in Mediterranean-type ecosystems have been discussed in recent reviews (Rundel 1981, 1982). In this paper we report on a series of experiments investigating such seasonal burning impacts on pure stands of a highly flammable and fire-adapted shrub, Chamaebatia foliolosa, on the west slope of the Sierra Nevada in California. We have two specific purposes in this study: first to demonstrate the direct effects of fire on stand productivity and nutrient uptake fluxes, and secondly to investigate the significance of fire seasonality on these processes.

Chamaebatia foliolosa Benth. (Rosaceae) is a low evergreen shrub 30-50 cm in height which forms relatively pure stands in a narrow transition belt between chaparral and coniferous forest zones along the west slope of the Sierra Nevada in California. The shrubs are evergreen, with heavily scented and glandular foliage. Individual leaves typically survive for only one year with old leaves gradually lost during the growing season as new leaves are formed. New growth in Chamaebatia is initiated in early May with new leaves being formed into July. Branch elongation continues into August. Peak seasonal stand biomass occurs around October. Stands are frequently under snow cover for 1-3 months during the winter.

The root system of Chamaebatia consists of shallowly branched rhizomatous roots. Individual shrubs are virtually impossible to delineate.

Fine roots are nodulated and may be active nitrogen-fixers (Heisey et al. 1980). Following fire the plants resprout from adventitious buds along the rhizomes, producing a dense stand of short stems. Frequently there are several hundred stems per square meter.

One of the interesting characteristics of Chamaebatia is its highly flammable nature. There are many anecdotal accounts of the species burning within a few hours of a rain storm or with snow still on the ground. Many structural and chemical characteristics of Chamaebatia promote its flammability. The finely dissected leaves and fine branch structure provide high surface to volume ratios and good convective air circulation. The high ether extractive content of the foliage, reaching a peak of 7-9% in late summer, suggests a chemical component of its flammability are the subject of a separate study.

2. MATERIALS AND METHODS

All field experimental burns were carried out in Sequoia National Park in a relatively pure stand of Chamaebatia foliolosa near the old Colony Mile Ranger Station at an elevation of 1615 m. This stand occurs on a south-facing slope of approximately 20° slope angle. Small trees of Quercus kelloggii are scattered through the study site and a few individuals of Calocedrus decurrens and Pinus ponderosa are present nearby. Each treatment plot consisted of a 10 x 10 m quadrat. Three seasons of experimental fires were carried out on 18 May, 19 July, and 12 October 1978. Spring and fall burns were ignited as backing fires to simulate the movement of upslope lightning fires down into the plots. The summer fire was a head fire to simulate a more intense burn. In each case, between 65 and 75% of the above-ground biomass of Chamaebatia was consumed by the fire including all leaf material. Unburned stems were virtually all killed by the fire, so that regrowth was

entirely from buds along rhizomes or at stem bases.

Each treatment plot plus a control plot was sampled for preburn biomass by harvesting 10 0.1 m^2 quadrats. Following each experimental fire the plot was resampled to determine the amount of above-ground biomass and litter consumed by the fire. Ash samples were collected from fixed area subplots to determine weights of deposition. The amount of above-ground biomass and its distribution by tissue types was resampled for all treatments at monthly intervals over the course of the study. These tissues were analyzed each month for nitrogen and phosphorus content. Soil samples, collected as composites of 30 sub-samples for 0-10 cm soil layers, were collected for each treatment at the same intervals and analyzed for soil nutrient concentrations. All nutrient analyses were carried out using methods described by Rundel and Parsons (1980).

Annual patterns of productivity and nutrient accumulation in above-ground biomass were calculated for the growth years ending in October. This month corresponds to the peak level of above-ground biomass following summer growth. Litter-fall was estimated as the difference between peak leaf biomass in October and low levels in April before new leaf initiation occurs. Root biomass was not calculated directly, but determined using an estimate of root-shoot ratio of 0.50. Production as used in this paper is clipping production of new growth, and thus does not include radial increments of woody growth.

3. RESULTS AND DISCUSSION

The 1978 annual cycle of biomass production for the control plot of *Chamaebatia foliolosa* is shown diagrammatically in Figure 1. The total above-ground biomass of 982 g m^{-2} is relatively small compared to typical Mediterranean-climate shrub communities. Nearby chaparral stands of *Adenostoma fasciculatum* reach up to five times this biomass. The above-ground biomass accumulation ratio (biomass divided by net growth)

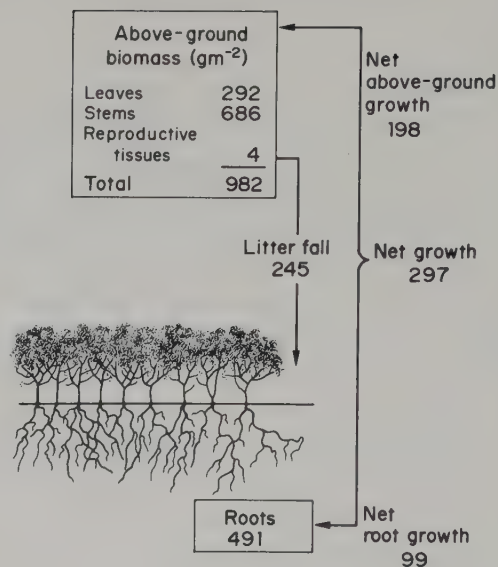


FIGURE 1. Annual cycle of biomass production in *Chamaebatia foliolosa*. Data for 1978 growing season.

of 4.96 is relatively low for Mediterranean-climate communities. Both above-ground biomass and biomass accumulation ratio are much more similar to published values for cold desert shrublands.

Because of the low canopy height of *Chamaebatia*, a relatively large percentage of biomass (30%) is in leaf tissue. Values of 10-20% are more typical for evergreen chaparral shrubs. Reproductive allocation in *Chamaebatia* is very low, with only 0.4% of above-ground biomass in flowers and fruits. This may reflect the primary reliance of this species on vegetative resprouting from underground rhizomes. Regrowth rates of foliage following fire are rapid. The spring burn plot reached a leaf biomass equal to that of the control plot after only two seasons of growth. Total above-ground biomass was considerably lower, however, since new stem tissue grew much more slowly.

Stimulated growth occurs in the first year of post-fire resprouting of both spring and fall burns

(Figure 2). For the 1978 growing season the productivity of the spring burn plot was nearly three times as great as that of the control plot. The summer burn plot, ignited in mid-growing season, had only about 40% of the production of the control plot. The fall burn plot during its first year of post-fire regrowth (1979) had a net above-ground productivity of over 160% of that of the control plot for the same year. The second year post-fire production for the spring and summer burns was slightly lower but not statistically different than the control plot.

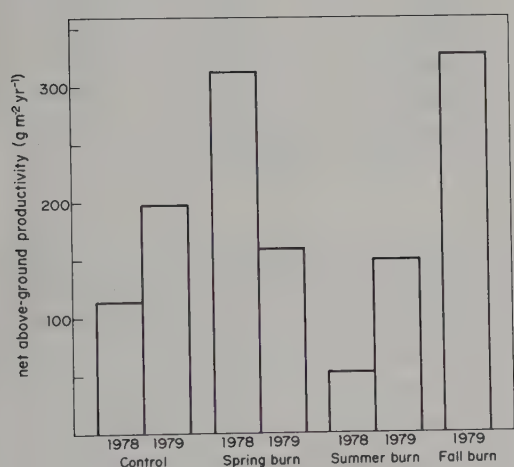


FIGURE 2. Net above-ground productivity in control and burn plots of *Chamaebatia foliolosa*

The 1978 annual cycle of nitrogen and phosphorus dynamics for the control plot of *Chamaebatia* is shown in Figure 3 in a manner similar to that for biomass dynamics. Since the nutrient content of *Chamaebatia* foliage is relatively high in comparison to that of most Mediterranean-climate shrubs, the nitrogen and phosphorus content per unit area of *Chamaebatia* canopy is comparable to coastal sage scrub or poorer chaparral shrublands in California. There are 9.13 g m^{-2} of nitrogen and 1.08 g m^{-2} of phosphorus in the above-ground biomass. The mean nitrogen content in October was 1.77% for leaves and 0.60% for stems. For phos-

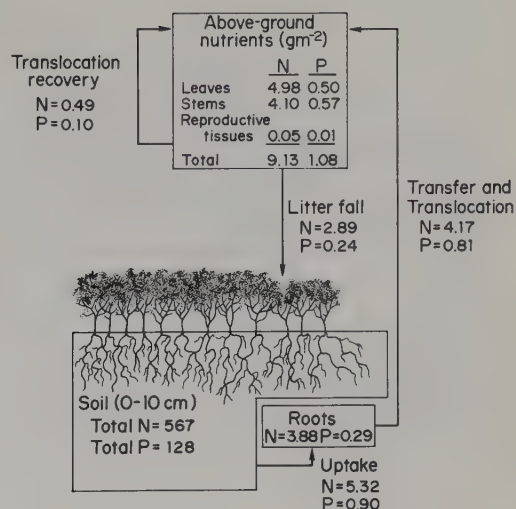


FIGURE 3. Annual cycle of nitrogen and phosphorus dynamics in *Chamaebatia foliolosa*. Data for 1978 growing season.

phorus the values are 0.17% and 0.08% respectively. The above-ground uptake of nitrogen over the 1979 growing season was 4.17 g m^{-2} . There was a loss of nitrogen in litterfall of 2.89%, for a net uptake of 1.28 g m^{-2} . For phosphorus there was an above-ground uptake of 0.81 g m^{-2} with a loss of 0.24 g m^{-2} in litter fall. Values for phosphorus are much more difficult to interpret than for nitrogen, however, since phosphorus has a highly variable seasonal pattern of mobility. The 1979 values of phosphorus uptake are much higher than those of the previous year, while uptake rates of nitrogen for the two years are quite similar.

In assessing the impact of fire on nutrient cycling processes, it is important to consider the primary effects of fire on nutrient fluxes. These primary effects are shown diagrammatically in Figure 4 by the heavy arrows. The combustion of above-ground biomass and litter compartments produces a very rapid decomposition which deposits large amounts of nutrient rich ash on the soil surface where it may be mineralized. Some of the nutrients formerly contained in the living and dead biomass, however, become volatilized during pyrolysis and are lost from

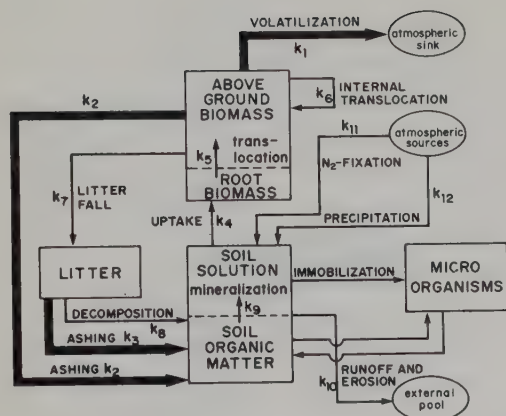


FIGURE 4. Nutrient cycling pathways for *Chamaebatia foliolosa*. Fluxes primarily affected by fire are shown by heavy lines.

the local site.

Nitrogen in particular is affected in this manner with up to 70% or more of total nitrogen volatilized in intense fires (see review in Rundel, 1981).

The importance of ash in recycling nutrients back into the soil can be seen by measurements of the nutrient content of post-fire ash for summer and fall burns (Table 1). While these total amounts

Table 1. Return of nutrients (mg cm^{-2}) through ash fall in summer and fall burns.

RETURN OF NUTRIENTS THROUGH ASH FALL (mg m^{-2})

	Summer burn	Fall burn
N-NH ₄	62.2	42.8
N-NO ₃	5.7	3.8
soluble P	142	97.1
Total N	3570	1870
Total P	490	420

of nitrate-nitrogen, ammonium-nitrogen, and acid-soluble phosphorus do not seem very large, they

are very significant in comparison to the existing pools of available nutrients in the upper 10 cm of soil (Table 2). Our soil nutrient data, not discussed in detail in this paper, confirms that these nutrients are rapidly mineralized into the upper soil horizon.

Table 2. Return of nutrients (% preburn soil concentrations for 0-10 cm) through ash fall in summer and fall burns.

RETURN OF NUTRIENTS THROUGH ASH FALL (% preburn soil concentrations, 0-10 cm)

	Summer burn	Fall burn
N-NH ₄	1560	718
N-NO ₃	358	178
soluble P	2332	1579
Total N	0.57	0.49
Total P	0.40	0.29

The net above-ground uptake of nitrogen and phosphorus, defined as the difference in the standing crops of nitrogen and phosphorus between October of each year, provides a comparative measure of the rates of nutrient uptake in control and burn plots. Such a comparison for the 1978 and 1979 growing seasons is shown in Figure 5 for nitrogen. The net above-ground uptake for the 1978 growing season immediately following the spring burn was nearly three times greater than for the adjacent control plot over the same period. The summer burn plot, burned in mid-growing season, had a much lower net nitrogen uptake than the control plot. During the 1979 growing season the first year of nitrogen uptake in the fall burn plot was considerably greater than in the control plot, following the same pattern as the spring plot the year before. Second-year nitrogen uptake (1979) in the spring burn plot was similar to that of the control plot, while the summer burn plot remained low in its second-year uptake. A very similar pattern is present for rates of net above-ground phosphorus uptake (Figure 6). First post-fire-year uptake in the spring burn plot (1978) and fall burn plot (1979) are significantly

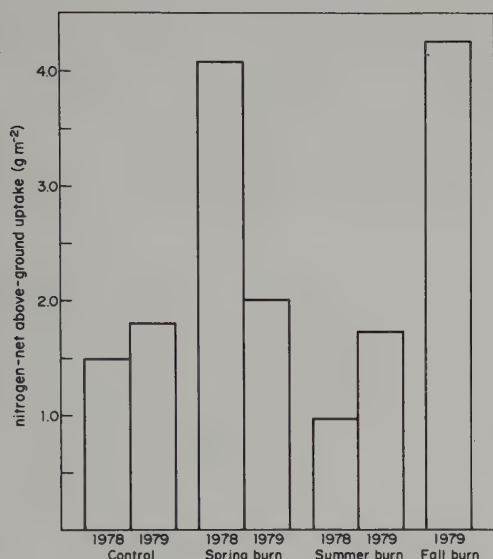


FIGURE 5. Net above-ground uptake of nitrogen in control and burn plots of *Chamaebatia foliolosa*.

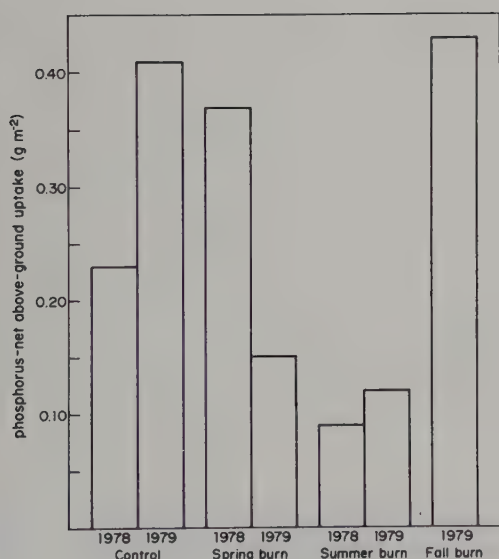


FIGURE 6. Net above-ground uptake of phosphorus in control and burn plots of *Chamaebatia foliolosa*.

higher than in the comparable years for the control plot. The summer burn plots had a significant depression of phosphorus uptake not only in the first but in the second year of post-fire regrowth.

In these comparisons of net uptake of nitrogen and phosphorus in the various treatments, it should be kept in mind that these are changes in net above-ground nutrient pools. Growth rates of uptake would include adjustments for litterfall losses and translocation recovery as shown in Figure 3. Thus gross rates of uptake in 1978 for the control plot is actually slightly higher than in the burn plot. Nevertheless the net uptake values provide a measure of the ability of the community to sequester nutrients in biomass compartments.

In summary then there are several important conclusions that can be made from this investigation of the post-fire responses of productivity and nutrient uptake in *Chamaebatia foliolosa*. The first major point is that fire does provide an important role in influencing nutrient cycling fluxes. The ash deposition data demonstrate that large amounts of available nitrogen and phosphorus are produced at the soil surface during fires. These nutrients are rapidly mineralized and produce enhanced rates of growth following spring and fall fires. The significantly higher concentrations of nutrients in post-fire growth in comparison to control plots suggests that luxury consumption of nutrients may be taking place. Our second major point is that seasonality of burning may be an extremely important determinant of post-fire regrowth. While the effect of spring (pre-growing season) and fall (post-growing season) fires clearly stimulate regrowth, summer burns (mid-growing season) appear to inhibit regrowth for at least two years.

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BIOMASS, PRODUCTIVITY AND SUCCESSION IN THE SCRUB OF THE DOÑANA BIOLOGICAL RESERVE IN SOUTHWEST SPAIN

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1. INTRODUCTION

The Doñana Biological Reserve is located between 36°55' and 37°3' N latitude and 6°16' and 6°34' W longitude on the western side of the Guadalquivir River in southwestern Spain.

The mediterranean climate of this region is modified in part by oceanic influence. Winter temperatures are mild with a daily mean of 9.3°C during the coldest months (January and December). Summer temperatures are high, with a daily mean of 23.9°C for July, the warmest month. Average annual rainfall is around 600 mm with maxima in both winter and early spring. Summer drought is severe, with no precipitation during July and August, and little if any in June and September. The area may be classified as thermo-Mediterranean attenuated (UNESCO, 1963).

The Reserve includes part of a large coastal plain partially covered with eolic sands. Two main complexes have been distinguished: the stabilized sands and the mobile dunes (Allier et al., 1974). This study was carried out in the stabilized sand complex.

The present-day topography consists of a series of ridges separated by depressions which are the remains of old dunes. Because of a shallow and almost horizontal water table and high substrate permeability, the tops of the ridges are arid, while the depressions are mesic with frequent winter flooding.

Matorral (scrub) is the predominant vegetation type. Species composition appears to be controlled by soil topography through the depth of the water table (Gonzalez Bernaldez et al., 1975), changing gradually from an open semiarid scrubland on the tops of the ridges with Halimium halimifolium, Rosmarinus officinalis, Halimium commutatum and Cistus libanotis as more abundant species, to a

heathland composed predominantly of Erica scoparia, E. ciliaris, Calluna vulgaris, and Ulex nanus in the depressions.

The present work is a study of the variation in the above-ground biomass and net productivity along the water table depth gradient. In addition, some aspects of post-fire succession on the ridges and depressions are examined.

2. METHODS

On an area where no fires had been recorded for at least 80 years, a 175 m transect was laid down. The transect included the maximum variation in scrub vegetation from that present on top of a ridge to that in a depression. At three points located 365, 200 and 90 cm over the water table (average summer depth), 15 plots of 5 m by 5 m were randomly located.

On every plot, the above-ground parts of all plants present were harvested separately. After drying at 80°C the weight of the current year's shoots, total leaf weight, and total wood weight fractions in a sample of individuals from each species and topographic situation were recorded. Total biomass was calculated from the total harvest (Martin de Agar, 1979). These data were used to estimate productivity and the ratios leaf biomass to wood biomass and new shoot production to total biomass.

Litter fall was estimated from 68 litter traps sampled at 1 month intervals for two years. The traps, each 350 cm² in area, were randomly distributed on the three topographic situations. Because the plant cover is less than 100% on the tops of the ridges, traps were placed under the canopies of randomly selected individuals of each

species, and the yearly litter production was estimated from the monthly sample weights and the species cover.

For the succession study, seven areas burned at different times were selected using aerial pictures and information from local residents. In each area the tops of the ridges and the depressions, respectively 365 and 90 cm above the average summer water table, were sampled separately. The numbers and sizes of plots were adjusted for different vegetation heights. The plots from the moisture gradient study were included in the calculations. The characteristics of the areas studied are shown in Table 3.

For each plot, dry weight measurements were determined for total above-ground parts and leaf and wood fractions.

3. RESULTS

3.1. Spatial pattern of productivity

The gradual change in the water table depth is associated with the spatial change in edaphic characteristics (Table 1). With increasing water table depth, the soil texture becomes coarser and water retention capacity decreases. Both total nitrogen content and cation exchange capacity are higher in the depressions than on the ridges.

The average biomass values are almost linearly related to the water table depth, ranging from 0.489 kg m^{-2} at 365 cm above the water table to 1.290 kg m^{-2} at 200 cm and 2.187 kg m^{-2} at 90 cm.

The pattern of new shoot productivity resembles that of biomass, with values of 0.086, 0.212 and $0.385 \text{ kg m}^{-2} \text{ yr}^{-1}$ at the same three sites.

The productivity to biomass ratios are similar on ridge tops and depressions (1.75 and 1.76), but the structure of the community changes along the gradient. The leaf to wood ratio is lower in the more mesic depressions. Annual litter production also declines with increasing water table depth. The values are similar to those for new shoot production.

3.2. Succession

Because most of the species are present at the first stage (unpublished data), the successional process does not occur as a species substitution. Thus, it would be more appropriate to speak of autosuccession rather than succession (Hanes, 1971).

As shown in Figure 1, the pattern of variation of biomass through time is similar on ridge tops and in depressions. In both cases, biomass reaches a maximum about 20 to 30 years after burning and then apparently declines (this decrease is not

TABLE 1. Site characteristics.

Site	Water table depth. cm (summer average)	Clay %	Silt %	Fine sand %	Coarse sand %	Water content at 0,3 atm. % dry weight	Water content at 15 atm. % dry weight	N %	Cation exch. capacity meq./100 g
Ridge	365	4,5	2,8	69,3	23,4	2,24	1,39	0,02	9,04
Slope	200	2,6	6,8	66,2	24,4	3,32	2,23	0,03	9,51
Depression	90	7,5	17,9	68,3	6,3	16,26	9,59	0,26	29,90

Productivity and biomass distribution at the three sites, ranging from xeric tops to mesic depressions are summarized in Table 2.

statistically significant). However, from the available data, it is not possible to determine whether biomass is decreasing gradually and

TABLE 2. Changes of some variables with topography.

Site	Biomass kg m ⁻²	New shoot kg m ⁻² year ⁻¹	Litter kg m ⁻² year ⁻¹	New shoot Biomass	Leaf Wood	Biomass accumulation kg m ⁻² year ⁻¹
Ridge	0,489	0,086	0,088	0,175	0,142	0,064
Slope	1,290	0,212	0,269	0,164	0,143	--
Depression	2,187	0,385	0,334	0,176	0,117	0,265

continuously, or whether there is a temporary decrease followed by stabilization.

The rate of biomass accumulation can be estimated from the slope of the biomass versus time curve. Using the mean biomass values, the estimated accumulation rates for ridges and depressions are 0,064 and 0,265 kg m⁻² yr⁻¹, respectively (Table 2).

The value of the leaf to wood ratio declines with time and reaches an asymptote about 30 years after fire (Fig. 2).

4. DISCUSSION

The results of the study of biomass and productivity reflect the existence of two close but very distinct communities.

The above-ground biomass and productivity values in the depressions are comparable to estimates for other mediterranean scrub communities in the literature (Jossaint, 1973; Margaris, 1976; Mooney, Rundel, 1979). The productivity values are higher than those reported for both English (Bellamy, Holland, 1966; Chapman, 1967; Miller, Miles, 1969) and Australian heath communities (Jones et al., 1969; Specht, 1969). In some cases, the reported values are even less than 0,265 kg m⁻² yr⁻¹, the minimum estimate of biomass accumulation derived from the slope of the biomass curve (Table 2).

Climbing to the tops of the ridges, the vegetation characteristics change gradually to communities whose biomass and productivity fall in the proposed range for tundra and desert formations (Rodin, Bazilevich, 1969; Lieth, 1973).

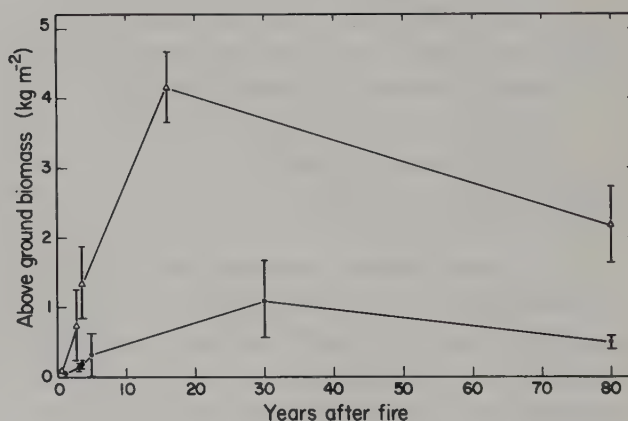


FIGURE 1. Biomass changes with time. Vertical bars indicate \pm standard deviation. Ridges (●), depressions (Δ).

The moisture gradient associated with the topography appears to be the main factor responsible for the change in community characteristics. Greater height above the water table and lower water retention capacity of the soil are responsible for prolonged water stress situations. During the summer, water potentials down to 8.1 KPa have been recorded for individuals growing on the tops of the ridges. In the same season, the values for individuals growing

TABLE 3. Site characteristics of the succession study.

Area	SO	CB	M	LD	Z	R	SO	CB	M	T	R
Site	R	R	R	R	R	R	D	D	D	D	D
Age (years)	0,6	3,7	3,8	5	30	80	0,6	3,7	3,8	16	80
Plot size (m ²)	1	1	1	1	1	25	1	1	4	4	25
Number of plots	8	5	12	12	10	5	11	12	6	5	6

in the depressions were about 0.8 KPa and never lower than 2.2 KPa (Merino et al., 1976).

The importance of water availability as a determinant of carbon gain in mediterranean ecosystems has been shown (Mooney, Dunn, 1970; Dunn et al., 1976). Prolonged stress situations on the ridge tops probably limit carbon gain during much of the year. This could account for the small productivity values observed.

To the moisture gradient effects it may be necessary to superimpose those of the nutrient richness gradient. However, the xeromorphic character and the wide spacing among individuals on the ridge tops suggest that water is the most important factor determining biomass and productivity differences with topography. In fact, in a nearby area with homogeneous edaphic characteristics, spatial and seasonal variation in water table depth explains most of the variation in productivity of *Pinus pinea* (Merino et al., 1976).

In this context, the constance of the productivity to biomass ratio is surprising. It might be predicted that increased fertility in the depressions would result in a higher value for this ratio. However, the leaf to wood ratio decreases, suggesting that the efficiency per unit of photosynthetic tissue is higher in

the depressions. This may reflect the greater fertility at these sites.

With regard to succession, it is interesting to note the shape of the curves. Although the difference between the penultimate and last points is not significant, the trends on both ridges and depressions are very similar, showing a decrease in biomass. According to Major (1974), there is a great deal of evidence from many ecosystems that biomass tends to decrease with time. Hanes (1971) has reported for the California chaparral an almost continuous decrease in biomass after the maximum. However, others have not observed this in scrub formations (Bellamy, Holland, 1966; Specht, 1969; Jones et al., 1969).

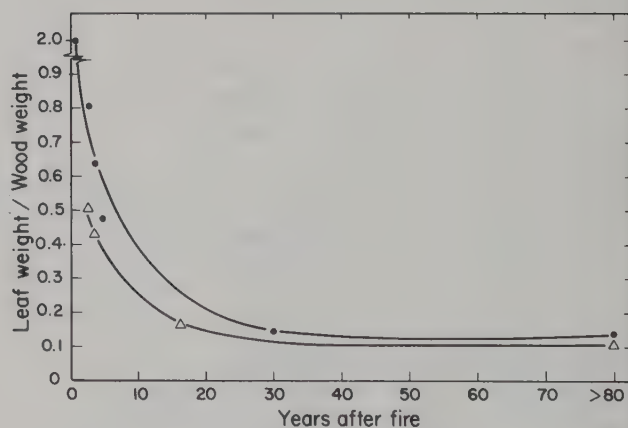


FIGURE 2. Changes in the leaf to wood ratio with time. Symbols as in Fig. 1.

The decrease in biomass combined with the apparently continuous decrease of the leaf to wood ratio indicates that productivity decreases after the biomass maximum is reached.

One possible cause of the biomass decrease in depressions may be the occurrence of structural changes associated with the age of individuals. After fire, the density of individuals increases, reaching a maximum at about 20 years (unpublished data). With the increase in size of individuals, there is a decrease in the light intensity in the understory. This decrease in light availability limits plant density in the understory.

The shape of the biomass curves could be a consequence of the evolution of productivity along a successional gradient. Peet (cited in Reiners, 1980) has summarized the evidence for bell-shaped rather than asymptotic productivity curves.

In Doñana, such changes in productivity could be explained by the large increase in nutrient availability after fire, combined with the nutrient accumulation capacity of the underground organs of some species. This pattern could account for the very vigorous regrowth of *E. scoparia* after fire (Martin Vicente, 1980). The underground organs of other species with no resprouting capacity should release the nutrients slowly during the decomposition process. A recycling mechanism such as this has been described by Borrows (1976) for mallee vegetation and for the Australian sclerophyll communities (Attiwill, 1974).

In addition, the high post-fire germination rates of some species (García Novo, 1977), especially on the ridges, could contribute to faster absorption of nutrients and higher early productivity.

Later, when the nutrient availability decreases as a consequence of absorption and leaching, the productivity will decrease to values determined for the pre-fire mineralization rates. The reduction in the ratio of productivity to rate of litter production caused by this decrease could be responsible for the decrease in total biomass.

According to Hanes (1971), the biomass decrease in the chaparral is caused by the accumulation of toxic substances. They cause the decreases in both germination and mineralization rates and, as a consequence, productivity decreases. Because the continuous productivity decrease causes a reduction in the ratio of productivity to rate of litter production, it may be possible to use it as an indicator of senescence. Values lower than 1 mean that the system is in a degenerative phase, and higher than 1 that it is a growth phase.

It appears that the degenerative process described by Hanes is not taking place in the 80-year-old scrub because litter production is very similar to new shoot production (Table 1). In addition, the field observations do not show any indication of degeneration; for example, the cover remains constant after about 15 to 20 years after fire. Thus, it seems that, at 80 years, productivity is stable, and the decrease in productivity that resulted in the apparent biomass decline shown in Figure 1 occurred soon after the maximum.

However, no succession was observed after 80 years. The absence of seedlings of new species is similar to the successional arrest observed in mature chaparral (Hanes, 1971).

In summary, the results suggest a decrease in net productivity with time related to decreases in both the leaf to wood ratio and biomass. The biomass maximum appears to be associated with a productivity maximum resulting from the temporary abundance of some resource (probably nutrients).

The lack of any apparent degenerative process associated with aging suggests that there will be no further decrease in productivity. In addition, the absence of successional changes preclude an increase in productivity (Odum, 1960). So it appears that within 80 years productivity in Doñana becomes stable and remains so for at least as long as the vegetation remains unburned. However, in the prediction of primary productivity of Doñana vegetation, it will be necessary to take into account the effects of the water table oscillation due to climatic variability (Merino et al., 1976).

SUMMARY

The biomass and productivity of the established sand dune complex of the Doñana Biological Reserve is described in relation to topography and time after fire.

The standing biomass and new shoot production appear to be controlled by soil topography through the depth of water table. Biomass and new shoot production appear to be linearly related to water table depth. Litter production shows a similar pattern, and values at each site are close to shoot production values.

Biomass accumulation rates are higher in depressions than in ridges.

Both a biomass decrease after 20 to 30 years and a decrease in the leaf to wood ratio indicate a successional decrease in productivity. However, in the older stage studied (80 years after fire) the ratio of productivity to rate of litter production is around 1, suggesting that the decrease in productivity is not continuous but takes place before this time. This decrease in productivity is probably determined by a decline in nutrient levels from high values immediately after fire.

In the depressions a decrease in light availability probably works in a similar way.

Finally, because there are no indications of both senile and posterior successional stages, it is suggested that productivity becomes stable within 80 years.

ACKNOWLEDGMENTS

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SPECIES STRUCTURE AND PRODUCTIVITY IN GRASSLANDS OF NORTHERN GREECE*

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1. INTRODUCTION

Grasslands are a major vegetation type in Greece. Their area is estimated to 1.7 million hectares and it represents about 13% of the total land of the country. Almost half of them are found in northern Greece (Macedonia and Thrace)(Ministry of Agriculture, 1961), where they occupy a variety of environments from sea level up to the subalpine and the alpine zones of the high mountains.

Of all the grassland types of Greece only the ones found in the alpine zone are climatically determined. The remaining types constituting more than 90% of the entire grassland area are considered as successional, derived mainly from oak forests after their destruction by uncontrolled cuttings, wildfires and overgrazing (Ganiat-sas, 1964; Horvat et al., 1974).

Several studies have been made concerning mainly floristic and sociological aspects of grasslands in Greece (Economidou, 1976). Systematic ecological work, however, is lacking. Such work is necessary if the structure and function of these ecosystems is to be understood. Moreover, their biological productivity needs to be known, since grasslands are the main grazing lands for livestock and wild animals and they are thus vital to the national economy.

This paper is a contribution to our knowledge of the structure and function of grasslands in northern Greece. It contains information on aerial productivity of plant species grown in three different ecological zones, and how this productivity is related to air temperature and rainfall.

* The assistance of Mrs. K. Karayiannakidou in identifying the plant species and of Dr. D. Analogides in the regression analysis is gratefully acknowledged.

2. DESCRIPTION OF SITES

The three sites were chosen along an elevation gradient in the central and eastern Macedonia so that they represent major, ecologically different, grassland areas (Fig. 1).



FIGURE 1. Northern Greece (Macedonia and Thrace) with the three grassland study sites.

One site was located on the low elevation zone, 10 km away from the sea coast and had an altitude of 60 m. The second site was inland, on a middle elevation area, and had an altitude of 650 m. The third site was located on the high elevation or subalpine zone, above the timber line, and had an altitude of 1500 m.

Although each site had the best soils of the area it represented, there were wide differences in the parent material and, consequently, in the physical and chemical properties of the soil among the three sites. In general, the high site had deeper soils, with higher acidity and organic matter content than the other two sites. However, all of them had soil depth equal to or greater than 30 cm.

The climate of northern Greece in general is of the mediterranean type (Balafoutis, 1977), but the three sites had quite different climatic conditions. According to the weather stations, adjacent to the experimental plots, long-term annual precipitation was 425 mm on the low site and 625 mm on the middle

site; long-term mean annual air temperature was 16°C and 13°C respectively on the two sites. For the high site, a temporarily established collective rain gauge gave about 1000 mm annual precipitation, a significant part of which was snow falling in the months from December to March. Air temperatures were estimated by using the lapse-rate developed by E.G. Vavliakis (personal communication) on the basis of the temperature recordings of the weather station on the middle site. Mean air temperature was found to be 8.6°C . Figures 2 and 3 show the monthly values of precipitation and air temperature for the study period on the three sites.

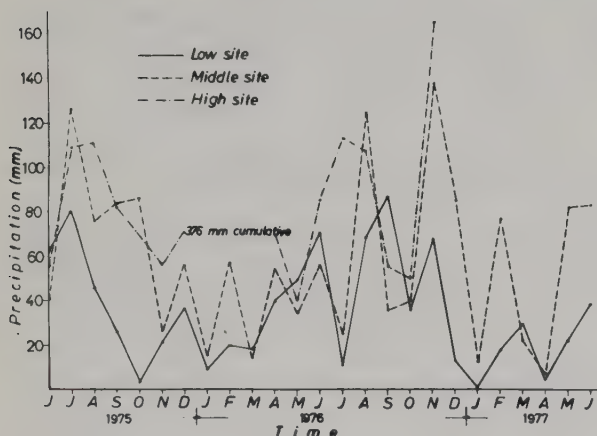


FIGURE 2: Monthly values of precipitation for the study period on the three sites.

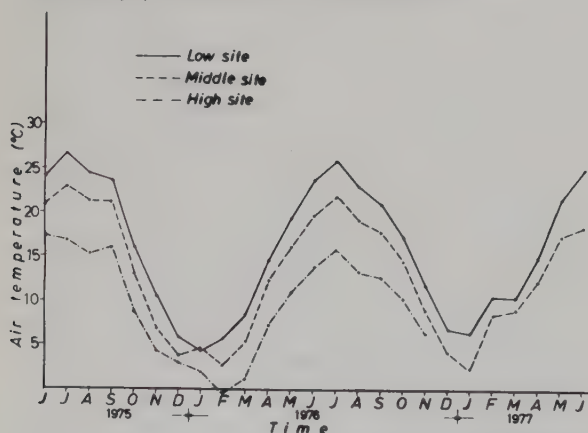


FIGURE 3. Monthly values of mean air temperature for the study period on the three sites.

As to the yearly variations, precipitation was below normal in 1975 (380 mm), above normal in 1976 (482 mm) and far below normal in 1977 (267 mm) on the low site. Also, 1976 was cooler (15.1°C) than the other two years. At the middle site, precipitation was above normal in 1975 (668 mm) and in 1976 (675 mm) and below normal in 1977 (497 mm); mean air temperature was lower in the two former years than in the latter. At the high site finally, precipitation was 1079 mm in 1975 and 991 mm in 1976 and mean air temperature 8.7°C and 8.0°C respectively for the two years.

These differences in climatic conditions among the three sites were reflected in differences on the growing conditions for the plants. For example, the thermal potential growing season, namely the number of consecutive days with a 15-day running-mean air temperature $\geq 4.4^{\circ}\text{C}$ (Sims et al., 1978), was different on the three sites in 1976, which was taken as a reference year. At the low site, it started on March 8 and ended on November 28, a total length of 262 days; at the middle site, it started on March 24 and ended on November 23, a total of 245 days; and at the high site, it started on April 13 and ended on November 22, a total length of 223 days. Vegetation was predominantly herbaceous on all sites. In addition, there were some shrubs sparsely distributed both at the low and middle sites. At the high site, however, only half-shrubs were found. Live-stock grazing was prohibited for at least 20 years on the low site, while the other two sites were only slightly grazed before the study was made. On the other hand, no grazing was allowed on all sites during the course of the study. Therefore, it can be considered that all three sites were representing natural, practically ungrazed grasslands.

3. METHODS

On each site an area of 250 m^2 was selected, where twelve plots corresponding to the twelve months of the year were randomly established. Each plot was 2X2 meters and was replicated three times. On the low and middle sites, the plots were placed in such a way so that the few scattered shrubs were avoided;

on the high site, the plots included some half-shrubs too, intermingled with the predominant herbaceous plants.

Measurements were started in June 1975, on all sites, but they were terminated in different months so that two growing seasons were covered for the species present. Ending months were July and June 1977, respectively for the low and middle sites and November 1976 for the high site. No measurements were taken on the latter site during the winter months and the month of March because of the snow cover.

Above-ground plant biomass was measured by the harvest method (Odum, 1971) on the 15th of each month. Three samples were taken from each plot by means of a quadrat 0.0625 square meters in size (Papanastasis, 1978). Vegetation was clipped to the ground level and placed in paper sacks. In the laboratory, the green (live) material was sorted by hand from the dead and it was separated by individual species. They were 9 species identified on the low site, 10 on the middle and 11 on the high site. The remaining, materially insignificant, species were identified by name and they were grouped into two categories: "other grasses" for the members of the grass family and "other forbs" for the members of all other families. Finally, the separated species and their groups were weighed after oven-drying for 48 hrs at 70°C.

4. RESULTS

4.1. Species characteristics

All sites were rich in plant species. Table 1 lists the species encountered in the experimental plots. This list is not exhaustive, since it does not include several rare species, which were not found in the sampling plots. Overall, there were 37 species identified on the low site, 40 on the middle and 33 on the high site. The majority of the species on all sites were forbs. Also, most of the species were annuals on the low site, while on the middle site there were only a small proportion; on the high site,

however, not a single one was annual. Finally, only a few species were common on two sites. The grasses Andropogon ischaemum and Chrysopogon gryllus were the main common species on the low and the middle sites; and Festuca ovina and Koeleria cristata the main ones on the middle and the high sites.

4.2. Growth patterns

The individual values of biomass for each species were averaged over the replications within the same sampling date. The resulted means are graphed on figures 4, 5 and 6, which present the growth curves of each species on the three sites. It is apparent that growth had a distinct seasonal pattern, different from one species to another and from one site to the other. Clearly, there were two groups of plants with different growth patterns on the low and middle sites. One group was the warm-season plants, namely the species which made their best growth during the warmer part of the growing season. In general, they started their growth early in the spring, peaked during the summer months and closed their cycle with the advent of the cold weather in late fall (growing season April to November). This group included the perennial grasses Andropogon ischaemum and Chrysopogon gryllus grown on both sites and the perennial forbs Dianthus viscidus of the low site and Thymus vulgaris and Teucrium hamaedris of the middle site.

The other group were the cool-season plants, namely the ones which made their best growth during the cooler part of the growing season. Generally speaking again, they started growing some time in the fall, continued slowly in the winter and rapidly in the spring, peaked in late spring and closed their cycle early in the summer (growing season November to June). This group included all the remaining plants on both sites, annuals and perennials. It must be noted that perennials had a longer growth cycle than annuals, which were dormant at least on the low site for a period of 3-4 months in the summer (Fig. 4).

On the high site, all species started their growth

TABLE 1. Plant species encountered in the experimental plots*

Low site	Middle site	High site
GRASSES	GRASSES	GRASSES
Annuals	Annuals	Annuals
<u>Avena sterilis</u> L.	<u>Bromus squarrosus</u> L.	—
<u>Bromus communatus</u> Schard.	Perennials	Perennials
<u>Hordeum asperum</u> Deg.	+ <u>Andropogon ischaemum</u> L.	<u>Anthoxanthum odoratum</u> L.
<u>Phleum tenue</u> Shard.	+ <u>Chrysopogon gryllus</u> Trin.	<u>Brachypodium pinnatum</u> Beauv.
<u>Triticum villosus</u> M.B.	+ <u>Festuca ovina</u> L.	<u>Bromus fibrosus</u> Hack
Perennials	+ <u>Koeleria cristata</u> (L) Pers.	<u>Calamagrostis montana</u> DC.
+ <u>Andropogon ischaemum</u> L.	<u>Phleum montanum</u> C. Koch.	<u>Deschampsia flexuosa</u> Trin.
+ <u>Chrysopogon gryllus</u> Trin.	<u>P. pratense</u> L.	+ <u>Festuca ovina</u> L.
FORBS	FORBS	<u>F. pilosa</u> Hall.
Annuals	Annuals	<u>F. varia</u> Haenke
<u>Anagalis arvensis</u> L.	<u>Cerastium pilosum</u> Sibth.	+ <u>Koeleria cristata</u> (L) Pers.
<u>Anthemis arvensis</u> L.	<u>Coronilla varia</u> L.	FORBS
<u>Asperula arvensis</u> L.	<u>Erodium cicutarium</u> L'Herit.	Annuals
<u>Convolvulus elegantissimus</u> Mill.	<u>Galium aparine</u> L.	Perennials
<u>Crupina crupinastrum</u> Vis.	<u>Geranium columbinum</u> L.	<u>Alchemilla pratensis</u> Sohm.
<u>Eryngium creticum</u> Lam.	<u>Lathyrus incospicuus</u> L.	<u>Asperula longiflora</u> W. & K.
<u>Euphorbia helioscopia</u> L.	+ <u>Medicago minima</u> L.	<u>Dianthus serratifolius</u> S.&Sm.
<u>Hymenocarpus circinatus</u> (L) Savi.	+ <u>M. tribuloides</u> Ders.	<u>Euphorbia gerardiana</u> L.
<u>Lagoseris sancta</u> (L) Maly	+ <u>Muscari comosum</u> Mill.	<u>E. silvatica</u> L.
<u>Lathyrus sativus</u> (L)	<u>Trifolium campestre</u> Schreb.	<u>Fragaria vesca</u> L.
<u>Leontodon fasciculatus</u> Nym.	<u>T. hirtum</u> All.	<u>Galium purpureum</u> L.
+ <u>Medicago minima</u> L.	<u>T. purpureum</u> Lois.	<u>G. verum</u> Scop.
+ <u>M. tribuloides</u> Desr.	<u>Vicia tenuifolia</u> Roth.	<u>G. verum</u> L.
+ <u>Muscari comosum</u> Mill.	Perennials	<u>Genista carinalis</u> Griseb.
<u>Nigella damascena</u> L.	<u>Achillea millefolium</u> L.	<u>Helianthemum vulgare</u> Lam.
<u>Ornithogalum umbellatum</u> L.	<u>A. tomentosa</u> L.	+ <u>Hieracium pilosella</u> L.
<u>Pastinaca sativa</u> L.	<u>Astragalus austriacus</u> Jac.	<u>Lathyrus niger</u> L.
<u>Senecio vulgaris</u> L.	<u>Calamintha vulgaris</u> Dacce.	<u>Leontodon asperinus</u> Boiss.
<u>Trifolium angustifolium</u> L.	<u>Campanula calaminthifolia</u> Lamk.	<u>Nepeta pannonica</u> Neillr.
<u>T. dalmaticum</u> Vis.	<u>Centaurea pectinata</u> L.	<u>Origanum vulgare</u> L.
<u>T. subterraneum</u> L.	<u>Dianthus carthusianorum</u> L.	<u>Primula elatior</u> Hill.
<u>Xeranthemum inapertum</u> L.	<u>Dorycnium herbaceum</u> Vill.	+ <u>Stachys germanica</u> L.
Perennials	<u>Hieracium cynosum</u> L.	<u>Thymus serpyllum</u> L.
<u>Alyssum murale</u> W.K.	+ <u>H. pilosella</u> L.	<u>T. tosevi</u> Vel.
<u>Dianthus viscidus</u> Ch. & Borry.	<u>H. pratense</u> Tausch.	<u>Trifolium alpestre</u> L.
<u>Hypericum perforatum</u> L.	<u>Hypericum olympicum</u> L.	<u>T. medium</u> L.
<u>Lastuca saligna</u> L.	+ <u>H. perforatum</u> L.	HALF-SHRUBS
<u>Scabiosa argentea</u> L.	<u>Lychnis coronaria</u> Desv.	<u>Rosa canina</u> L.
<u>Stachys germanica</u> L.	<u>Potentilla argentea</u> L.	<u>Vaccinium myrtillus</u> L.
<u>Teucrium polium</u> L.	<u>P. hirta</u> L.	
<u>Verbascum sinuatum</u> L.	<u>Poterium sanguisorba</u> L.	
	<u>Rumex acetocella</u> L.	
	<u>Teucrium chamaedrys</u> L.	
	<u>Thymus vulgaris</u> L.	

* Species preceded by a plus (+) are common on two sites.

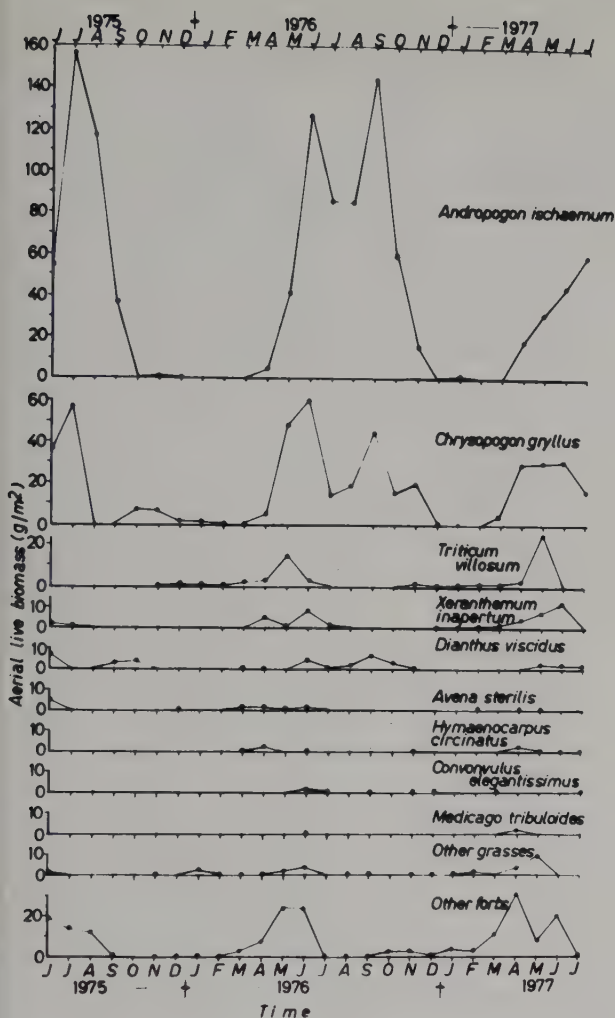


FIGURE 4. Growth curves of species on the low site.

in late spring due to the severe winter period, although some of them remained green under the snow cover, such as *Festuca varia* (Papanastasis, unpublished data). Again, most of them made their best growth in the cooler part of the growing season. Exceptions were the perennial forb *Dianthus serratifolius* and the half-shrub *Vaccinium myrtillus* which behaved as warm-season plants. The form of the growth curve for the majority of the species on all sites was of the unimodal type. However, some species gave bimodal growth curves in one or both growing seasons studied. These

were basically warm-season plants. For example, *Andropogon ischaemum* and *Chrysopogon gryllus* at the low site had bimodal curves in 1976 with one maximum in June and another in September as opposed to 1975, when they both had only one maximum in July. On the middle site, the former species had unimodal curves in both years, while the latter only in 1976. Analogous was the performance of the other warm-season plants (Fig. 4, 5, and 6).

As expected, the common grasses *Andropogon ischaemum* and *Chrysopogon gryllus* on the low and middle sites made their growth relatively earlier in the season on the former than on the latter site, but on both sites the former species grew later in the season than the latter (Fig. 4 and 5).

Similarly, *Festuca ovina* and *Koeleria cristata* grew earlier on the middle than on the high site (Fig. 5 and 6).

4.3. Dominant vs. sub-dominant species

Despite the large number of species on all sites only a few of them made the bulk of the production. Table 2 shows the percentage contribution of the three dominants to the total biomass throughout the sampling period. It is characteristic that these three species were all grasses and that they comprised more than 50% of the total biomass in most of the sampling dates and, especially, in the rapid-growth months. *Andropogon ischaemum* was the dominant species on the low site making at times 92% of the total biomass. On the middle site, however, it was less important as compared to *Festuca ovina* which was leading species on this site. *Chrysopogon gryllus* was much more important on the low than on the middle site. The annual grass *Triticum villosum* was important on the low site only during the winter months.

On the high site, *Calamagrostis montana* was the leading species followed closely by *Festuca varia*, while *Brachypodium pinnatum* ranked third. The remaining sub-dominant species were secondary in terms of contribution to the total biomass on all sites.

TABLE 2. Contribution (%) to the total biomass of the three dominant species in each of the three sites.*

Year	Month	Low site			Middle site			High site		
		<u>Andropogon</u> <u>ischaemum</u>	<u>Chrysopogon</u> <u>gryllus</u>	<u>Triticum</u> <u>villosum</u>	<u>Andropogon</u> <u>ischaemum</u>	<u>Chrysopogon</u> <u>gryllus</u>	<u>Festuca</u> <u>ovina</u>	<u>Calamagrostis</u> <u>montana</u>	<u>Festuca</u> <u>varia</u>	<u>Bruchypodium</u> <u>pinnatum</u>
1975	J	44	28	0	20	10	27	14	10	8
	J	68	25	0	24	16	22	18	18	8
	A	91	0	0	42	0	24	22	23	12
	S	92	0	0	19	0	18	26	15	9
	O	0	62	0	4	22	9	15	21	9
	N	14	75	3	0	6	33	0	66	1
	D	7	37	30	0	1	37	-	-	-
1976	J	0	4	18	0	0	34	-	-	-
	F	0	17	33	0	0	27	-	-	-
	M	0	2	18	0	1	55	-	-	-
	A	13	14	8	0	0	43	0	55	-
	M	31	37	11	4	0	19	13	12	-
	J	54	26	1	15	14	17	22	25	7
	J	84	13	0	6	13	32	35	8	8
	A	80	18	0	41	8	16	30	20	13
	S	74	23	0	29	5	24	26	16	16
	O	75	19	0	37	1	6	16	28	11
	N	40	48	3	1	12	28	2	45	0
	D	0	32	18	0	3	50	-	-	-
1977	J	21	2	2	0	0	57	-	-	-
	F	0	0	15	0	0	54	-	-	-
	M	0	24	5	0	0	33	-	-	-
	A	20	33	3	1	31	23	-	-	-
	M	28	27	22	1	5	13	-	-	-
	J	40	28	0	11	11	11	-	-	-

* Dashes mean that no sampling was done in the respective months.

4.4 Yearly changes

Biomass of the individual species changed not only from one sampling date to the next within the same season, but also between years for the same sampling date. This resulted in changes of the structure of grasslands between seasons, which were very pronounced on the low site, less

pronounced on the middle and of intermediate intensity on the high site.

In general, all species had higher biomass in 1976 than in 1975 or 1977 on the low site. An exception was found for the grass Triticum villosum and the forb Xeranthemum inapertum, which had higher yields in 1977 than in 1976. Also, Andropogon ischaemum

had higher peak biomass in 1975 than in 1976 (Fig. 4). All these resulted in differences both in the timing and in the size of the peak biomass of the community as a whole. Thus, peak biomass was 227 g m^{-2} in 1975 and it was attained in July; in 1976, it was higher (233 g m^{-2}) but it was attained in June; in 1977, it was far lower (112 g m^{-2}) and it was attained in May.

On the middle site, some species had higher peak biomass in 1975 and some in 1976 or 1977. However, the peak biomass of the whole community was highest in 1977 (248 g m^{-2}) as opposed to 1976, when it was 237 g m^{-2} and to 1975, when it was lowest (204 g m^{-2}). This must be attributed to the aggressive tall annual legume *Vicia tenuifolia*, the biomass of which increased from 21 g m^{-2} in June of 1975 to 49 g m^{-2} in 1976, and to 93 g m^{-2} in June of 1977 (Fig. 5).

On the high site, most species and, especially, the dominant grasses, had higher peak biomass in 1975 than in 1976. This resulted in a far higher peak biomass of the whole community in 1975 (604 g m^{-2}), attained in August, than in 1976 (415 g m^{-2}), which was attained in July (Fig. 6).

4.5. Net community production

In the multi-species communities one harvest at the time of the peak biomass is likely to underestimate productivity, since the individual species mature at different times (Kelly et al., 1974). Therefore, summation of the peaks of the individual species is a more appropriate method for grasslands with a long growing season (Singh et al., 1975). Since all sites studied represent multi-species grasslands with wide differences in the timing of the peak biomass of the individual species, the "summation of the peaks" method was used to get net community production (Odum, 1971). This method was applied only in 1976, because only in this year were full growth cycles available for all species.

It was found that net community production was 264 g m^{-2} on the low site, 305 g m^{-2} on the middle and 558 g m^{-2} on the high site. These figures are

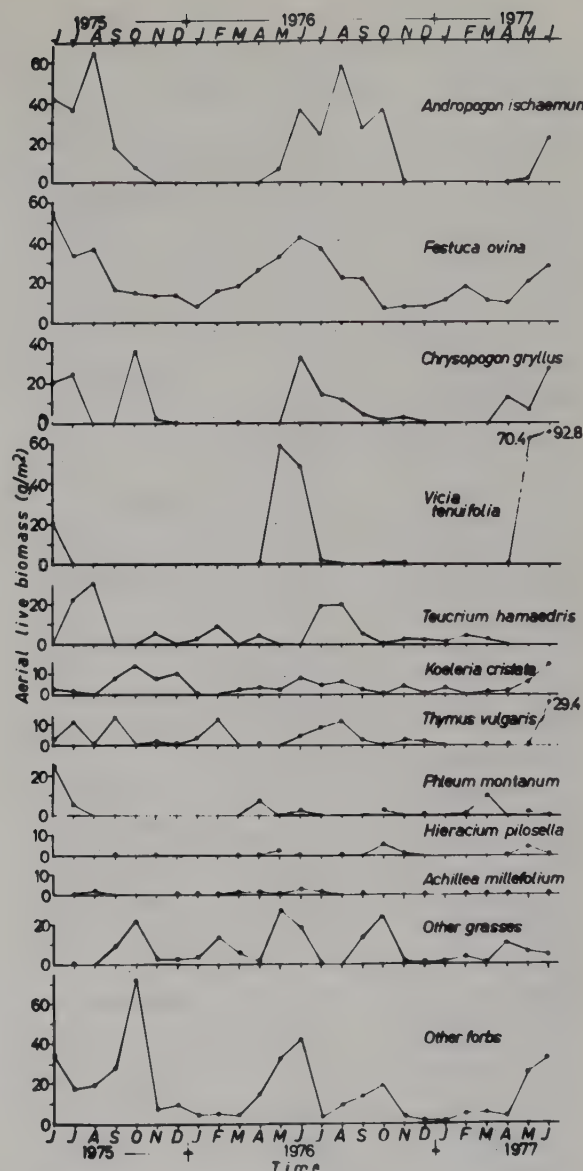


FIGURE 5. Growth curves of species on the middle site.

13%, 29% and 34% higher than the ones of the single harvest for the year 1976 already mentioned above. Analogous increases (25–50%) were found in the grasslands of the western U. S. (Lauenroth, 1979).

4.6. Growth rates

In order to compare the production capacity of the individual species within and between sites, it was assumed that all plants started their growth early

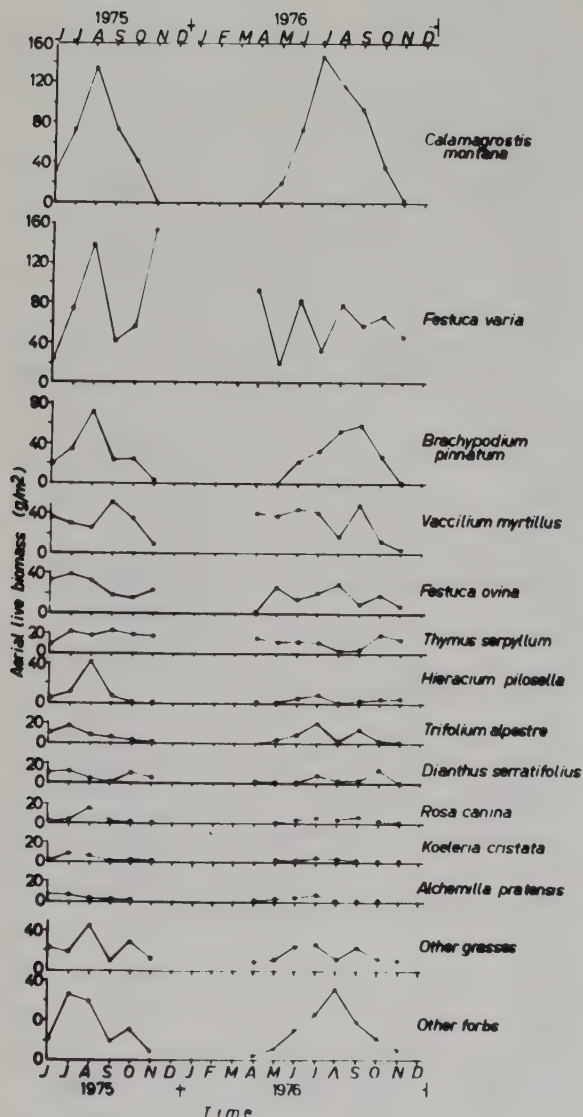


FIGURE 6. Growth curves of species on the high site. (From December to March no measurements were taken).

in the spring. This is a realistic assumption, since even the species starting to grow in the fall, namely the cool-season plants, did not produce much until the early spring, when their growth became rapid (Fig. 4 and 5). Therefore, the average growth rate of each species was calculated for the time period from the beginning

of the thermal potential growing season in each site, up until the date when their peak biomass was attained. The results for 1976, are shown on table 3. It is apparent that the species with the highest rate growth was *Calamagrostis montana* of the high site, followed by *Festuca varia* also of the high site, and by *Andropogon ischaemum* of the low site. Among the forbs, the most productive was the annual legume *Vicia tenuifolia* of the middle site. Maximum or peak growth rates are considered as indices of the photosynthetic capacity of different grasslands under particular environmental conditions (Sims and Singh, 1978). These rates were different both among species and sites and they were attained at different time intervals (Table 3). *Andropogon ischaemum* of the low site had the highest rate and was followed by the two dominant grasses of the high site.

The interesting finding is that the species of the low site attained their peak rates in a shorter time period than the ones of the middle site, and these in a shorter time period than the ones of the high site. The period for the low site was from March 16 to June 15 with most of the species having peak rates from May 16 to June 15. At the middle site, the period started a month later and finished two months later than at the low site with most of the plants having their maximum rate again in the interval from May 16 to June 15. At the high site, finally, the period was extended from May 16 to October 15. Analogous were the results for the average and maximum growth rates of the entire communities in each site, calculated with the same methodology as for the individual species (Table 3). It turned out that the high site was the most productive grassland with an average rate 56% higher than the middle and 90% higher than the low site. The middle site was 21% more productive than the low one.

4.7. Productivity and weather parameters

Plant growth depends largely on the specific environmental conditions of the site involved, especially to air temperature and rainfall (Lieth, 1975; French, 1979). In order to find out how these two main weath-

TABLE 3. Average and maximum rates of increase in green biomass ($\text{g m}^{-2} \text{ day}^{-1}$) of the species in each of the three sites for the year 1976.

Site	Species	Average rate	Time period for average (days)	Maximum rate	Time interval for maximum
Low	<u>Andropogon ischaemum</u>	1.27	100	2.79	May 16-Jun.15
	<u>Chrysopogon gryllus</u>	0.60	100	1.43	Apr.16-May 15
	<u>Iriticum villosum</u>	0.20	69	0.38	Apr.16-May 15
	<u>Xeranthemum inapertum</u>	0.08	100	0.22	May 16-Jun.15
	<u>Dianthus viscidus</u>	0.05	100	0.15	May 16-Jun.15
	<u>Avena sterilis</u>	0.02	100	0.05	May 16-Jun.15
	<u>Hymenocarpus circinatus</u>	0.06	39	0.06	Mar.16-Apr.15
	<u>Convolvulus elegantissimus</u>	0.01	100	0.04	May 16-Jun.15
	<u>Medicago tribuloides</u>	0.01	100	0.01	May 16-Jun.15
	Whole community	2.35	100	3.35	May 16-Jun.15
Middle	<u>Andropogon ischaemum</u>	0.40	146	1.08	Jul.16-Aug.15
	<u>Festuca ovina</u>	0.50	85	0.31	May 16-Jun.15
	<u>Chrysopogon gryllus</u>	0.39	85	1.04	May 16-Jun.15
	<u>Vicia tenuifolia</u>	1.13	54	1.95	Apr.16-May 15
	<u>Teucrium hamaedris</u>	0.13	146	0.64	Jun.16-Jul.15
	<u>Koeleria cristata</u>	0.10	85	0.19	May 16-Jun.15
	<u>Thymus vulgaris</u>	0.08	146	0.14	May 16-Jun.15
	<u>Phleum montanum</u>	0.03	85	0.08	May 16-Jun.15
	<u>Hieracium pilosella</u>	0.05	205	0.08	Apr.16-May 15
	<u>Achillea millefolium</u>	0.04	85	0.09	May 16-Jun.15
	Whole community	2.85	85	3.43	May 16-Jun.15
High	<u>Calamagrostis montana</u>	1.58	94	2.46	Jun.16-Jul.15
	<u>Festuca varia</u>	1.31	64	2.11	May 16-Jun.15
	<u>Brachypodium pinnatum</u>	0.38	156	0.71	May 16-Jun.15
	<u>Vaccinium myrtillus</u>	0.32	156	1.02	Aug.16-Sep.15
	<u>Festuca ovina</u>	0.24	125	0.85	May 16-Jun.15
	<u>Thymus serpyllum</u>	0.10	64	0.50	Sep.16-Oct.15
	<u>Hieracium pilosella</u>	0.09	94	0.12	May 16-Jun.15
	<u>Trifolium alpestre</u>	0.22	94	0.38	Jun.16-Jul.15
	<u>Dianthus serratifolius</u>	0.08	94	0.36	Sep.16-Oct.15
	<u>Rosa canina</u>	0.04	156	0.09	May 16-Jun.15
	<u>Koeleria cristata</u>	0.05	94	0.10	Jun.16-Jul.15
	<u>Alchemilla pratensis</u>	0.08	94	0.12	Jun.16-Jul.15
	Whole community	4.46	94	6.61	Jun.16-Jul.15

er parameters affected the growth cycles of the three dominant species in each of the three sites, non-linear regressions were run according to the standard statistical procedures (Steel, Torrie, 1960). Monthly values of air temperature and rainfall were fitted to the monthly values of biomass of each species throughout the growing season. The period tested was from April to November, 1976 for all species except for Triticum villosum of the low site and Festuca ovina of the middle site, which were tested for the period November, 1975 to June, 1976.

The model used was of the form:

$$Y = b_0 + b_1X + b_2X^2 + b_3X^3$$

The results are presented on table 4. They show that most of the species on all sites had a high correlation with air temperature. However, this correlation was rather linear, as it was indicated by the statistical significance of the linear components of the above model and the non-significance of the quadratic and cubic components. An exception was found for Triticum villosum, which had a cubic relationship with air temperature. Chrysopogon gryllus of both sites and Festuca varia of the high site gave a poor

correlation, probably due to the limited data used or to a more complex relationship that exists between their growth and air temperature than the one tested.

On the contrary, rainfall gave poor correlations with almost all species, except Andropogon ischaemum of the low site, and Calamagrostis montana and Brachypodium pinnatum of the high site. Their relationship though was rather quadratic than linear or cubic.

In general, Festuca ovina had the highest correlation with air temperature and Calamagrostis montana the highest one with rainfall.

5. DISCUSSION

The results of this study suggest that the grasslands of northern Greece are no different from the grasslands of the world, at least in some general structural features, such as the dominance of grasses in the plant cover and in the canopy biomass despite their far lower numbers as compared to forbs (Coupland, 1979a). On the other hand, they indicate the importance of the particular environmental factors in determining their structure and productivity.

TABLE 4. Correlation coefficients (R^2) for the linear, quadratic and cubic components of the regression between the aerial live biomass of the dominant species in each of the three sites and selected weather variables for the growing season in 1976 (see text for explanations).

Site	Species	Air temperature			Rainfall		
		Linear	Quadratic	Cubic	Linear	Quadratic	Cubic
Low	<u>Andropogon ischaemum</u>	0.57**	0.60	0.73	0.16	0.61*	0.61
	<u>Chrysopogon gryllus</u>	0.13	0.24	0.56	0.32	0.33	0.34
	<u>Triticum villosum</u>	0.34	0.40	0.79*	0.22	0.31	0.65
Middle	<u>Andropogon ischaemum</u>	0.42*	0.45	0.55	0.01	0.05	0.53
	<u>Chrysopogon gryllus</u>	0.38	0.48	0.56	0.00	0.09	0.12
	<u>Festuca ovina</u>	0.89***	0.92	0.93	0.19	0.27	0.52
High	<u>Calamagrostis montana</u>	0.84***	0.88	0.89	0.05	0.82**	0.84
	<u>Festuca varia</u>	0.03	0.04	0.10	0.03	0.04	0.06
	<u>Brachypodium pinnatum</u>	0.44*	0.49	0.57	0.00	0.54*	0.58

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$

The fact that the majority of the species encountered on the three grassland sites were cool-season plants may be attributed to the long-term overriding effects of the mediterranean climate of northern Greece, with its mild and rainy winters and the hot and dry summers (Balafoutis, 1977).

However, the summers are not completely dry on the study sites. For example, the proportion of the annual precipitation that fell in the summer period of 1976 was 37% on the low site, 32% on the middle and 31% on the high site. Although this high proportion is not a usual case (Papanastasis, unpublished data), it does indicate that there is some rainfall in the summer even on the low site. This rainfall combined with the higher temperatures relatively to the high site may explain why the low site was dominated by warm-season grasses. By contrast, the high site was dominated by cool-season grasses apparently due to its cooler climate as compared to the low site. Finally, the middle site being intermediate in climate was dominated by both warm-season and cool-season grasses. The same kind of distribution is also found in other parts of the world, such in the western U.S. (Sims et al., 1978). More important though are the physiological differences and the functional roles of these two groups of plants. According to Williams (1974), the major photosynthetic pathway C-3 (Benson-Calvin) corresponds with cool-season response, while pathway C-4 (Hatch-Slack) corresponds with warm-season response. Moreover, C-4 plants have higher photosynthetic capacity and consequently higher productivity, higher competitive ability, better adaptation to stress environments and more efficient use of water than C-3 plants (Black, 1971).

Andropogon ischaemum and Chrysopogon gryllus are both C-4 plants (Waller, Lewis, 1979). This may explain their higher productivity relatively to other species on the low and middle site and their capacity thus to dominate over broad ecological zones, of which the one represented by

the low site seems to be the optimum.

Yet, Andropogon ischaemum appeared to have higher productive capacity and better correlation with air temperature and rainfall than Chrysopogon gryllus. This may in part be due to a better structure of the leaves of the former species, in terms of water storing parenchyma, intercellular airspaces and peripheral reticulum, which enables it to withstand adverse environmental conditions (Eleftheriou, Noitsakis, 1978).

Another structural difference of the low site as compared to the high one was the presence of the annual species in the former and the absence of them in the latter. This is attributed to the particular environmental conditions of each site (Ganiatsas, 1964). Despite their richness, however, annuals contributed relatively little to the total biomass, except in the winter and early spring months, when they were the only plants growing. On the middle site, the few annual plants played an insignificant role, apart from Vicia tenuifolia, which tended to increase over the years for reasons not yet explored. It appears, therefore, that going from the low elevation to the high elevation zone there was an elimination of the annual plant component and a replacement of the dominant warm-season grasses by cool-season ones.

Above-ground productivity, though, was increased with elevation, although the growing season was respectively decreased. Part of the high production of the high site may be due to its deeper soil as compared to the other two sites. However, there is no doubt that environmental conditions, especially precipitation, played the major role. Precipitation, was increased with elevation as productivity did. This close relationship between precipitation and production has been documented by several studies in other grassland types of the world (Le Houerou, Rosté, 1977; Gutman, 1978; Sims, Singh, 1978). Precipitation seems to have been the main reason for the yearly variations in the peak biomass in each of the three sites, too. The low site had the highest peak biomass in 1976, a relatively wet year, and the lowest in 1977, a relatively dry year.

The same was on the middle site, although the impressive linear increase of the biomass of Vicia tenuifolia from 1975 to 1977 obscured the above relationship. Finally, the high site had higher biomass in 1975, a relatively wet year, than in 1976, a relatively dry year. However, besides precipitation other environmental factors must have influenced the above variations. This may explain the different response of some species, such as Triticum villosum of the low site, Andropogon ischaemum of the middle and Calamagrostis montana of the high site, which had higher peak biomass in the dry than in the wet years. Analogous results were found in other grasslands of the world (French, 1979).

Contrary to the yearly changes of the peak biomass, the seasonal variations of biomass and especially the growth rate of the individual species was affected more by air temperature than by rainfall, as it was shown by the regression analysis. Uresk et al. (1975) and Britton et al. (1978) found that soil temperature was the main factor relating to growth in grasslands of the U.S., while soil moisture was the main one: suggested by Gutman (1978) for Israel. Since the data used in the regression analysis were restricted to only one growing season and to only a few species, a more detailed study would be needed to thoroughly investigate the relation between growth and environmental factors in the grasslands of northern Greece.

Comparing the three sites, yearly variations were more pronounced on the low site than on the other two higher ones. This may be attributed in part to the wider variations in rainfall of the low elevation zone and in part to the significant annual plant component of the low site. It is well known from studies in the annual grasslands of California (Biswell, 1956; Heady, 1958), that annual plants are extremely vulnerable to the weather changes and, consequently, highly variable from one year to the next.

Although the grasslands of the low and the high sites had rather distinct structures, this was

not the case with the middle grassland, which had common structural elements with both the other two sites. Such elements were the dominant species Festuca ovina, a subdominant of the high site, and Andropogon ischaemum and Chrysopogon gryllus, both dominants of the low site, as well as annual plants from the low site (Table 1). This confirms the statement made by Ganiatsas (1964), that the middle elevation grasslands have species coming from both the low and the high elevation zone.

The facts that the middle site was co-dominated by the two main dominant species of the low site, that it had annual plants, and, that its productivity differed less from the low than from the high site suggest that middle grassland is ecologically closer to the low than to the high grassland.

The question that remains to be answered is how the grasslands of northern Greece are compared to other grassland types of the world in terms of net above-ground primary production. From the studies of the International Biological Program on 40 grassland types of the world has come out that the net annual shoot production ranges from 84 g.m^{-2} on semiarid tropical climates to $2,430 \text{ g.m}^{-2}$ on subhumid temperate climates under natural irrigation (flooding) (Coupland, 1979b). This Program has not included comparable types to the ones studied in northern Greece, namely perennial grasslands with mediterranean-type climate. Nevertheless, the net annual shoot production obtained at the three sites in 1976 corresponds on the average (375 g.m^{-2}) to the values of the temperate grasslands of the world, with the low site being closer to the semiarid climates and the high site closer to the more humid and mountain areas of northern Europe.

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PART FOUR

BIOMASS UTILIZATION

Utilization of biomass of the mediterranean-type ecosystems, in the areas of the Earth where they occur, differed in the past both in the methods used and in the intensity of use.

The ancient civilizations, developed all around the Mediterranean basin, were based exclusively for thousands of years on the use of biomass for energy and organics. Besides, the agricultural revolution which started much earlier there than in all the other climatically similar regions, 8000-10,000 years ago, and the recurrent fires and the overgrazing effect led to a wide conversion of natural ecosystems to agricultural land. In our times, as a result of the increased demand and the shortage of liquid fuel, there has developed there a serious attempt for reevaluation of the capabilities of these systems as energy producers. Nevertheless, the differences from region to region and from country to country, lead to differentiations of the policies followed as far as it concerns the energy problem. For example, in the developing countries of north Africa the matter is how to reduce biomass utilization because this uncontrolled activity in this place favours desertification. Thus, in countries like Libya, Algeria and Tunisia, rich in oil fuel, the attempt was to persuade the population to use oil instead of biomass as fuel.

The situation in the developed countries of southern Europe as well in California and Australia is totally different and consequently, there has developed a trend to use for energy biomass from natural ecosystems, agricultural residues and energy plantations. Exploitation of agricultural residues can be put into work immediately while energy plantations are less promising since they are competitive with agriculture for the use of arable lands. On the other hand, the possibility of biomass utilization from the natural vegetation, offering many advantages, seems quite feasible.

The recurrent fires in the mediterranean systems cause severe problems. For this reason, it has been proposed since long to reduce the accumulated fuel by prescribed burning techniques. However, these techniques lead to great losses of energy and organics. But if they are replaced by harvesting techniques they could possibly result to benefits both economic and environmental. The articles presented in this session concern proposals and methods of application centered upon biomass use for energy. No doubt, it is a very promising field of research expected to be greatly developed in the near future.

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BIOMASS AND NET PRIMARY PRODUCTIVITY OF PORTUGUESE FORESTS

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1. INTRODUCTION

In Portugal, as elsewhere, after the energy crisis, forests started to be regarded with a new interest. Due to this attitude arose the necessity of more information concerning our forest resources and we have recently begun an effort to acquire this knowledge. The present paper reflects the first steps in this direction.

The purpose of this article is to establish the preliminary estimates of biomass and net primary productivity (NPP) of Portuguese forests. The values established are derived from our national forest inventory, forest yield tables, our knowledge about the portuguese forests in comparison to other forests studied elsewhere and about which values of the biomass of components have been published.

Forest biomass studies are in their initial stage in Portugal. We are primarily concerned with the study of exotic forest ecosystems due to the reaction of environmentalists to impacts of their presence. In our Department (Forestry) we are carrying out an integrated project devoted to eucalyptus (*E. globulus*) stands.

We will propose some estimated figures of biomass of forest residues generated by the utilization of our forest resources. Comparative values of NPP derived from our yield tables and those supplied by the Montreal model are also presented.

2. PORTUGUESE FOREST RESOURCES

Forests occupy approximately one third of

the country. The greater density forest is found in the Central Region which is between the Douro and Tagus Rivers (1.4 million ha), followed by the Southern Region (1.2 million ha). As expected, the present situation of the forest area in the country is the result of a process where human influence had a paramount role. Although the distribution of the forested land is predominantly influenced by ecological factors, social and economic factors have also made their contribution.

Forest biomass and NPP are estimated according to table 1. Due to their particular conditions values for cork oak woodlands (*montados*) are not included (625200 ha)

TABLE 1. Portugal forest biomass and NPP (dry matter)

Forest type	Area 10 ³ ha	Biomass 10 ³ t	NPP 10 ³ t/yr
Maritime pine (<i>P. pinaster</i>)	1300	84931	6883
<i>P. pinea</i>	40	1696	85
Eucalyptus (<i>E. globulus</i>)	208	12603	2475
Holm oak (<i>Quercus ilex</i>)	536	19149	288
Several conifers	39	1683	85
Several hardwoods	139	3539	106
Mixed stands	17	392	16
Total	2279	123993	9938

We may estimate that 8% is the biomass growth of Portuguese forests and each portuguese individual has available approximately one ton of biomass (dry matter) yearly.

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3. ESTIMATIONS OF NPP FROM EMPIRICAL MODELS

The Montreal model was used to estimate the NPP for the Portuguese territory. We merely used a map with isolines of real evapotranspiration and substituted these values for those calculated of NPP (fig. 1).

To check the predictability of the Montreal model in our conditions we compared the values estimated from its application with those derived from maritime

pine yield tables. This is exhibited in table 2. We multiplied the timber growth (volume u.b.) from yield tables by $.6 \times 1.7$ to obtain NPP (dry matter). NPP values obtained from the Montreal model are always higher than those derived from mean annual increment (MAI) given by yield tables. Only in Foja, the NPP obtained from current annual increment (CAI) is higher than from the Montreal model.

TABLE 2. NPP from the Montreal model and derived from *P. pinaster* yield tables
t d.m./ha/year

Place (nº indicates the localities in fig.1)	NPP from the Montreal model	Site quality	Density nº of trees/ /ha	NPP from MAI _{max}	NPP from greatest CAI _{max}
1. Lima e Neiva (Morais, 1971)	12,9-14,4 > 14,4	H ₅₀ =20m	1111 950 710 1100	7.0 6.7 6.4 6.6	8.1
2. Foja (Martins, Cabral, 1970)	12,0-12,9	H ₅₀ =23m H ₅₀ =19m H ₅₀ =15m	460 570 845	8.5 5.8 3.1	13.4
3. Leiria (Carrascalão, 1969)	11,1-12,0	H ₅₀ =25m H ₅₀ =20m H ₅₀ =15m H ₅₀ =10m	295 350 435 700	8.1 5.4 3.2 1.5	8.8
4. Ribatejo (Goes, 1975)	11,1-12,0	H ₅₀ =22m H ₅₀ =19m H ₅₀ =10m	- - -	8.2 6.4 5.0	10.0
5. Ponte de Sor (D.G.S.F.A., 1969)	10,2-11,1	-	650	4.6	7.0
6. Caia (Lopes, 1967)	10,2-12,0	H ₅₀ =13m H ₅₀ =12m H ₅₀ =11m	- - -	4.2 3.8 2.6	

4. FOREST RESIDUES

We will attempt to establish the amount of forest residues generated by:

1. Wood harvesting
2. Forest industries
3. Final consumption

and the level of their reuse.

4.1. Residues from wood harvesting

The forecasted biomass value of pine residues are given in table 4 and those of eucalyptus residues in table 5.

TABLE 4. Biomass of residues from pine woods (dry matter). 10^3 t

	1980	1985	1990
Roots and stumps	515	533	572
Tops and branches	219	226	242
Leaves	110	113	121
Understory	63	65	69
	907	937	1004

TABLE 5. Biomass of residues from eucalyptus stands. 10^3 t

	1980	1985	1990
Bark (d.m.)	148	237	333
Branches and leaves	264	422	586
Thinnings from stumps	20	32	44
Tops (d.m.)	102	163	227

The biomass of pruning from cork oak stands amounts to 275 thousand tons (annual average values). Only 40% of the virgin cork is harvested and utilized. Virgin cork extraction is still a manual operation that has become non-profitable and has thus been abandoned.

We may estimate the total biomass of residues from wood harvesting and cork oak pruning at approximately 2 million tons. We have not been able to establish the amount of residues from thinnings.

There is a growing interest in forest residues, mainly for energy purposes. The demand for wood for combustion is increasing in Portugal. Bakeries and ceramics for the building industry are returning to wood as a fuel, as opposed to fueloil, and must account for 60% of the wood and plant residues as a fuel. In some regions of Portugal, the pulp industry starts competing with wood fuel purchasers who are now buying pulpwood.

Wood and other plant residues account for about 4% of the energy produced in Portugal which is equivalent to 250 thousand tons of fueloil to the value of 60 million dollars. Here are included 275 thousand tons from cork oak pruning (charcoal production) equivalent to 68 thousand tons of fueloil to the value 16 million dollars. The chemical industry uses approximately 80 thousand tons of eucalyptus leaves per year.

4.2. Residues from forest industries

The main bulk of residues from forest industries derives from sawmills. Sawmills residues are forecasted according to the following table.

TABLE 6. Biomass of residues from sawmills. 10^3 t

	1980	1985	1990
Residues	554	625	693

It is expected that the pulp industry in the next fifteen years will recycle sawmill residues as much as 442 thousand cubic meters of equivalent roundwood per year and the woodpanel industry 148 thousand cubic meters.

The pulp industry produces 64% of the electricity it uses from residues (10% ave

rage for the Portuguese industry). In their effluents the same industry throws into the environment 60 thousand tons of organic matter of which 15 thousand tons are non cellulosic carbohydrates.

4.3. Recycling of forest final products

The only available information with regards to the reuse of forest final products concerns recycled paper.

With regards to the population density the rate of recovery of used paper should be 30 to 35%. In 1977, 145 thousand tons were recovered which is equivalent to a rate of 37%. The reused paper represents 30% of all fiber consumed by the paper industry.

5. PRELIMINARY INFORMATION ON PHOTOSYNTHETIC CHARACTERISTICS OF *EUCALYPTUS GLOBULUS*

As we wrote above, we are undertaking an integral research project on *E. globulus*. This species is an important forest resource in the portuguese economy and a spreading feature of our rural landscape. Some preliminary results on photosynthetic characteristics of *E. globulus* have just been obtained by the gas-exchange method, utilizing an IRGA. Data were obtained at the Centro de Fruticultura Laboratory at Alcobaça (Portugal), using individual adult leaves in an aerated cuvette. Before sunrise shoots were carefully cut under water, transported to the lab and maintained with the tip in water. Leaf water potential was ca. 0 bar at arrival to the lab and was never recorded below ca. - 9 bar under transpiring conditions. Net photosynthesis has the highest observed value ($24 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$) at a leaf temperature of 28 to 29°C , for a Photosynthetically Active Radiation (PAR)

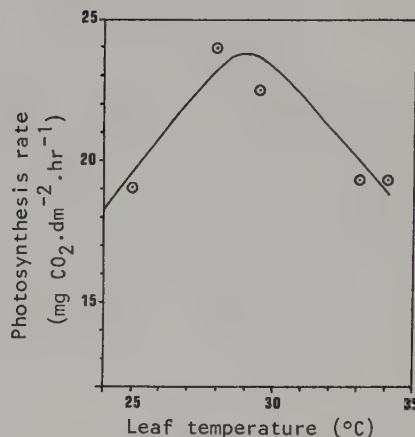


Fig.2 - Response of net photosynthesis of adult leaves of *E. globulus* to temperature, under saturating light conditions.

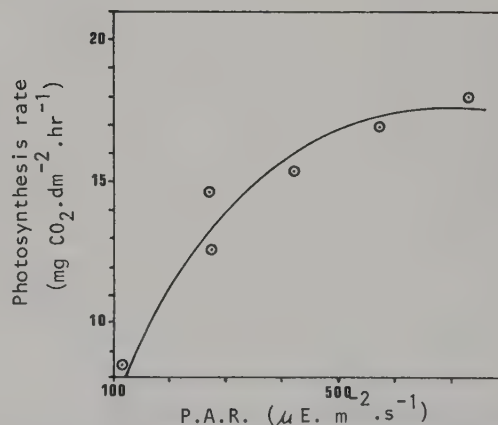


Fig.3 - Response of net photosynthesis of adult leaves of *E. globulus* to P.A.R., at 24°C .

flux of $730 \mu\text{E.m}^{-2}.\text{s}^{-1}$, assumed to be saturating (Fig. 2). However, at leaf temperature of 24°C the saturation net photosynthesis rate ($18 \text{ mg CO}_2.\text{dm}^{-2}.\text{hr}^{-1}$) is attained at a PAR flux of $580 \mu\text{E.m}^{-2}.\text{s}^{-1}$ (Fig. 3).

In table 7 we include some values of net photosynthesis, from the literature, for comparison. Some other species of the *Eucalyptus* genus seem to have values of net photosynthesis in the same range as

6. FINAL REMARKS

We think that the shortage of fuels and materials and thus the growing interest in renewable resources will put new pressure on the ecosystems of our region. To cope with this situation we need to increase our knowledge about these systems and our capability to manage them without jeopardizing their integrity. The understanding of the production process (mechanisms and patterns) of the ecosystems, within

TABLE 7. Selected values of net photosynthesis for trees and mediterranean shrubs

Species	Temp. ($^{\circ}\text{C}$)	Radiation $\mu\text{E.m}^{-2}.\text{s}^{-1}$	Net photosynthesis $\text{mg CO}_2.\text{dm}^{-2}.\text{hr}^{-1}$	Reference
<i>E. maculata</i>	24	800	14,5	Mooney et al. (1978)
<i>E. pilularis</i>	"	"	15,9	"
<i>E. saligna</i>	"	"	12,8	"
<i>E. blakelyi</i>	"	"	25,3	"
<i>E. melliodora</i>	"	"	26,7	"
<i>E. gracilis</i>	"	"	36,7	"
<i>E. socialis</i>	"	"	17,2	"
<i>P. deltoides</i>	30	1800	30 (aprox)	Drew, Bazzaz (1979)
<i>Populus</i> cv Unal	25	800-1000	17 (aprox)	Ceulemans, Impens (1979)
<i>Ceanothus greggii</i>	15	1801-2300	13,5	Oechel, Lawrence (1979)
Mediterranean shrubs from Cali- fornia and Chile and <i>Arbutus unedo</i>	25	saturating	12 to 18	Gigon (1979)

ours in similar temperature and saturating radiation. Our results also have the same magnitude as the references for other higher productive plantation trees as *Populus* (Ceulemans, Impens, 1979) and for some Mediterranean shrub species (Gigon, 1979) when temperature and light conditions are also similar. It strongly suggests that our results must be improved in further research especially since we want to model productivity with them.

this new context, gains a paramount relevance today.

Although we looked for the establishment of the amount of forest residues we do not advocate their indiscriminate use. Any program of reuse of residual should not be implemented without a careful study of its several impacts (Barreto, 1980 b).

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UTILIZATIONS OF MEDITERRANEAN FOREST BIOMASS FOR MAKING ENERGY AND ORGANICS

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1. THE YIELD

Recoverable biomass from mediterranean forest is varied in quality and quantity. Sylviculture yields 3 basic kinds of residue :

1.1. Non commercial thinnings :

In young stands of *Pinus halepensis*, the amounts of residues range from 25 to 45 t.ha⁻¹ fresh weight, plus 10 to 20 tonnes of possibly recoverable pulpwood.

In 30 or 40 year old stands of *Quercus ilex* or *Quercus lanuginosa*, the conversion of coppice to high forest produces 15 to 30 t. of slash plus 20 to 30 t. of fuelwood. (See Fig.1).



FIGURE 1. Conversion of coppice to high forest.

1.2. Logging slash residues :

The slash resulting from clear cutting of high forest varies according to the age and the species of the trees.

In spite of the fact that adult exploitable forests are rare in France we estimate that the available biomass represents 50 to 200 % of exploitable wood i.e. from 35 to 100 t.ha⁻¹ fresh weight, the greatest amounts coming from coniferous stands, especially *Pinus pinea* stands. (See Fig.2).



FIGURE 2. Slash resulting from clear cutting.

The slash resulting from clear cutting of coppice is generally less than 30 t.ha⁻¹ (20 to 30 t.) when the commercial wood crop is close to 80 steres or 40 t. (for instance in a 35 year old coppice of *Quercus ilex*).

1.3. Fire break brush control :

Fire breaks cover about 5 to 10% of inflammable forests areas; they are usually laid out along roads and in the best conditions of accessibility. This means that they represent the greatest available source of biomass in French mediterranean forests. (See Fig.3).



FIGURE 3. Fire break.

When the ground is cleared for the first time, it is possible to recover a large quantity of biomass, varying according to the floristic associations and generally ranging between 10 and 50 t.ha⁻¹ fresh weight. (See Tab.1).



FIGURE 4. Tractor chipper

TABLE 1. Recoverable biomass of different floristic associations at the first ground clearance of fire break.

Floristic association			recoverable biomass (t.ha ⁻¹ fresh weight)
Calcareous soils	<i>Quercus coccifera</i>	20 cm	15-20
		30 cm	18-22
		40 cm	20-25
		50 cm	24-35
		60 cm	33-40
		80 cm	46-53
		100 cm	55-67
	<i>Ulex parviflorus</i>	80-90 cm	10-20
		100 cm	15-30
		110-110 cm	25-40
Non calcareous soils	<i>Quercus coccifera</i> and <i>Ulex parviflorus</i>	40 and 20 cm	25-32
		50 and 20 cm	30-40
		60 and 20-30 cm	37-48
		70 and 20-30 cm	42-50
		80-90 and 20-40 cm	45-55
	<i>Rosmarinus officinalis</i>	25 years	18
	<i>Quercus ilex</i>	very clear	9
		clear	13-16
		dense	14-23
	<i>Erica arborea</i> and <i>Arbutus unedo</i>	50-70 cm	10-15
		70-100 cm	15-30
		100-150 cm	30-40
Non calcareous soils	<i>Erica scoparia</i> and <i>Calluna vulgaris</i>	150-250 cm	40-60
		50-70 cm	25-35
Non calcareous soils	<i>Cistus monspelliensis</i> and <i>Cistus salvioefolius</i>	30-50 cm	15-40
		80-100 cm	10-20

The annual growth of these floristic associations ranges from 0.5 to 2 t.ha⁻¹.year⁻¹ on calcareous soils and from 2 to 4 tonnes on non calcareous soils. With a 2 or 3 year cutting cycle, each harvesting represents 1 to 5 t.ha⁻¹ on calcareous soils and 4 to 10 t.ha⁻¹ on non calcareous soils.

2. THE HARVESTING

The present method of harvesting this biomass necessitates using a chipper after cutting the trees, tops and bushes. (See Fig.4).

The best existing machines are tractor chippers, mounted directly on the three-point hydraulic lift of a standard tractor, producing fine grain chips (their density is generally about 0.3 t.m⁻³) (See Fig.5), with a capacity of 2 to 10 m³ of chips per hour, according to the kind of material and the power of the tractor (30 to 90 H.P.).



FIGURE 5. Fine grain chips.

The current cost of the chips produced in France ranges from 40 to 70 U.S.\$.t⁻¹ for dense vegetation (for instance, first fire break brush control) and from 70 to 140 \$.t⁻¹ for light vegetation, plus the transport cost around 0,1 \$.t⁻¹ km⁻¹.

It depends particularly on the origin of the biomass and the harvesting time : 20 working days for logging slash residues, 30 working days for non commercial thinnings and 40 working days for fire break slash (the cost of recovery and chipping is only 10 to 20 % of the harvesting cost).

Mobile machines for harvesting and chipping forest biomass do exist, but they are not equipped to deal with mediterranean conditions and slash recovery. In France, at present, a machine is being studied capable of clearing undergrowth in rocky, sloping and dense vegetation conditions, which will save energy and will supply chips at less than 20 \$.t⁻¹.

3. MAKING OF ORGANICS

Farmers in mediterranean regions have for a long time used brush and forest wastes to make artificial manure. Leaves and small wood substances (except for highly resinous material) were mixed with stable litter and aromatic plants. This small-scale method has been adapted and is used to treat the biomass now recoverable by chipping. Chips obtained are laid out in windrows (See Fig.6), watered when necessary to keep the working compost at the proper moisture level and turned over every month to obtain in 12 to 18 months, according to the size of chips, enough decayed organics to be used in surface dressing. The cost price of this kind of compost ranges between 100 and 200 U.S.\$.t⁻¹.



FIGURE 6. Compost windrow.

Experiments employing industrial methods are underway. They use either a composter where aerobic fermentation is controlled and quickened, or inoculations of fixed bacteria extracted from the

stomach of termites, plus additions of mineral and nitrogenous substances. With these processes, working time to achieve the same result can be reduced to 1 or 2 months.

Several analyses of compost without additives show that the proportion of major elements (in percent of dry weight) range from :

Nitrogen (N)	0.3 to 1.0 %
Phosphorus (P_{2O_5})	0.1 to 0.2 %
Potassium (K_2O)	1.5 to 3 %
Magnesium (MgO)	0.5 to 1.8 %
Calcium (CaO)	2 to 13 %

Consequently, this compost has to be regarded as an organic improvement comparable to peat, which it could replace, for certain agricultural or horticultural uses (nurseries for instance).

Some tests made in Switzerland have shown that it cannot be regarded as manure or fertilizer, because employed just as it is, even in great quantity ($700 \text{ m}^3 \cdot \text{ha}^{-1}$), it could cause negative results to some market-garden crops, in spite of a low C/N ratio, owing to the kind of carbon. On the other hand, we have made experiments in France by surface dressing of small amounts on a young forest plantation (30 kg of compost per tree) which have proved, after 2 years, that there was an increase of height around 35% for *Cedrus atlantica* and 45% for *Robinia pseudoacacia*. However supplying and dressing compost have raised the planting price more than 50%.

4. MAKING OF ENERGY

There are several methods of recovering energy from forestry slash chips :

4.1. The dry method

Chips may be burnt in traditional wood heating equipment or in sawdust-woodwaste heating equipment. Studies have shown that this solution is competitive (in view of the current

oil price) if the cost of chips, carriage inclusive, is lower than $50 \text{ U.S. \$} \cdot \text{t}^{-1}$, which is possible in certain conditions. Nevertheless, we can note this price is higher than the one obtained with energy planting (*Arundo donax* for instance) or even with rational logging of coppice for energy.

Another way, often better, may be found with slow combustion of wastes, i.e. pyrolysis or gasification. 1 tonne of wood with 10% humidity, corresponding to a potential energy of about 16,000 MJ, burnt in a fixed-bed gas producer, supplies a gas which, used as a fuel in a dual-fuel engine, gives 1 Kwh of electric energy. If, besides, we recover heat contained in exhaust fumes (FIAT-TOTEM system) and if we convert electric energy into heat by using a "heat pump", from 1 tonne of wood we can obtain more than 15,000 MJ, which permits the highest possible recovery.

4. . The wet method

While making compost, we may recover a part of the heat given off during fermentation (temperature often exceeds 60°C .) by warming water which is circulated inside the pile.

For instance, we may set some concentric spirals of black polyethylene pipes inside a cylindrical pile of compost. (See Fig.7). Several experiments have shown unfortunately that such a system is not very powerful ($40 \text{ watts} \cdot \text{t}^{-1}$ and only produces low calories (45°C . warm water) which means that is not very useful for producing energy, even if we disregard the equipment and man-power price for fitting up the system.

By anaerobic fermentation, it is possible to produce methane from forestry waste. First tests made in France, have shown that 1 m^3 of chips (i.e. about 0.3 t.) could produce every day 0.3 to 0.4 m^3 of biogas during 5 months (at about 50% of methane), the time of half decomposition being close to 1.5 month. The rate of this production is so

slow because of the high proportion of lignin in the wood, also the cost price of digesters and tanks becomes prohibitive if a continuous output throughout the year is to be ensured (3 digesters are necessary). Methanisation of forestry waste is only valid if one has already got the equipment, which is used for instance for manure or straw, and is out of use for several months.



FIGURE 7. Recovery fermentation heat.

5. CONCLUSION

Current research in France shows that there are several possible agronomic or energetic uses of the mediterranean forest biomass. Their value is very variable : it depends mainly on man-power, raw materials and fuel prices. It depends too, to a lesser extent, on technology.

In any case, it must be remembered we can only valorize waste, i.e. biomass which is not already used, in particular for timber, industrial wood or pulwood.

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BIOMASS YIELD OF SHORT-ROTATION PLATANUS SPECIES IN GREECE
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1. INTRODUCTION

Short-rotation and intensive culture of American sycamore (Platanus occidentalis L.) has gained considerable interest since its inception by McAlpine et al (1966). The system calls for plantations by seedlings or cuttings in close spacing, which can be harvested by machines repeatedly on cycles of 3 to 5 years. After each harvest, of the above-ground portions of the trees, the stumps remain intact and resprout, thus regenerating the plantation. This process can be repeated 4-5 times and then should start by new planting all over again. It is difficult to define close spacing, because so many alternatives have been suggested, but as it comes out from the published data, any arrangement that provides less than one squaremeter of growing space to each stool is very close (Steinbeck 1980). The trend, in American short-rotation forestry research, is towards longer rotations and wider spacings.

This kind of plantations, initially destined to maximize production of hardwood fibers, may very well satisfy the objectives of energy forestry. Photosynthesis, which is dependent upon solar radiation, is the basic process for the storage of solar energy. Today it is widely accepted that short-rotation, intensive culture, good capacity of vegetative propagation and genetically improved varieties are the most important premises for successful energy plantation (UK - ISES 1979). Platanus species combine all the necessary

specifications, mentioned above, and more than that there exist extensive research work, concerning methods of propagation, harvesting, yield etc. especially for American cycamore.

In Greece Platanus orientalis is a species exhibiting considerable plasticity, growing on a variety of soils and climates all over the country, from low elevation to high altitudes. Moreover, it can be propagated vegetatively and planted without difficulty and also hybridize readily with introduced Platanus occidentalis. It was, therefore, considered that breeding and selection could produce high yielding varieties capable to establish short-rotation plantations for fibers or energy. The country is deficient in wood production and also introduces all the necessary quantity of oil, thus biomass plantations could be of great importance.

In this presentation the results of biomass production will be given, in a progeny test plantation of Platanus orientalis, P. occidentalis and P. acerifolia, six years after planting.

2. MATERIAL AND METHODS

The plantation was established with 1-0 seedlings during March 1972 on a site near Lamia (Lat. $38^{\circ} 57'$, Long. $22^{\circ} 10'$, Alt. 80m). The planting material came from seeds sown in an experimental nursery on the year before, representing 21 open pollinated families, 10 of Platanus orientalis, 10 of P. occidentalis and 1 of P. acerifolia. The P. orientalis seeds were collected randomly from trees growing in natural stands

from south to north Greece. The P. occidentalis seeds were imported from U.S.A. and the 1 family of P. acerifolia originated from seeds collected in north Greece, from a tree being the second generation of an old introduction in the country (Panetsos 1972). The site is along the Sperchios river, but quite far from its flooding zone, which used to be a nursery of the forest service for a long time. Its productivity is not high in comparison to the typical natural Platanus sites of this area, and also the ground water is low so that cannot stand growth of that species without watering during the growth season, at least the first years after planting. The site was plowed and disked prior to planting. No fertilizers were used before or after the establishment of the test, since our aim was to find genetic differences among the testing material, avoiding interactions such as genotype-fertilizer.

The design used was 4 randomized complete-blocks, with 25 seedlings per plot at spacing 1X1m., isolated by a buffer zone of the same material. The plantation was regularly irrigated during the growth season and also cultivated each year, until the third year, after which the growing seedlings shaded out the competing vegetation. In February 1979 the plantation was clear cut, at 4 to 8 cm above the ground-line, so that the remained stumps would provide coppice sprouts for the next cycle. The trees of each plot were bundled and weighed (without leaves) in the field immediately after cut. The same was repeated at the end of June of the same year, so that the weight of fresh and air dried biomass was recorded, by plot, family and species. For missing plants assessment was made on the basis

of the total weight of the plot.

3. RESULTS AND DISCUSSION

The estimated total green and air dried weight, after six complete growing seasons, is presented in table 1. The estimation is based on plot data, excluding border plants, and has been converted to weight per hectare/year. The weight comprises stem and branches but not leaves, since the cut was performed during the dormant season (February). According to J.R. Soucier et al (1972), the proportion of leaves to the total green weight for American sycamore at age 4 and spacing 1,2 by 1,2 meters, has been estimated to be 12 percent. Air dried-weight, appearing in the table, comes from actual measurements and corresponds to loss of moisture content in the average 36,7 percent for American sycamore, 41 for P. acerifolia and 40 percent for P. orientalis.

Survival exceeded 93 percent for P. occidentalis and P. acerifolia, but varied considerably among families of P. orientalis, which indicates sensitivity of that particular species to microenvironment of the test site. This could also be related to the origin of the families, since as it has been mentioned in previous chapter, the families originate in various geographical areas of the country.

Analysis of variance performed shows the existence of highly significant differences in yield between species, and also significant among families within the species. The higher green weight yield was 18,78 tonnes per hectare/year produced by P. acerifolia, which corresponds to about $3,7 \times 10^7$ Kcal/ha/yr (IDRC-MR3, 1979). Yields from this initial rotation is in general lower than those expected from subsequent coppice rotation. They were estimated from first coppice crops of sycamore to be about 45 percent greater

than those from the seedlings (G.R. Dutrow 1971). Growth of the original seedling stand for four or more years before harvest resulted in more vigorous sprouts than those from younger age seedlings. It is therefore anticipated that in our case the yield will be increased accordingly in the subsequent rotations.

TABLE 1. Estimated green and air dried yield, of stems and branches, per hectare/year

Species and Families	Tonnes/hectare/year	
	Green weight	Air-dried weight
P.occ.no 65	13.85	8.77
" 91	14.43	9.13
" 96	17.45	11.03
" 97	14.51	9.18
" 113	15.68	9.22
" 115	13.98	8.85
" 116	16.27	10.30
" 121	12.48	7.90
" 128	12.47	7.89
" 131	14.68	9.29
\bar{X}	14.58	9.23
P.ac. no 8	18.78	11.08
P.or. no 20	13.31	7.99
" 23	15.70	9.42
" 26	12.71	7.63
" 29	13.01	7.81
" 38	10.20	6.16
" 39	13.86	8.32
" 45	14.51	8.71
" 50	13.23	7.94
" 53	11.25	6.75
" A ₁	11.80	7.08
\bar{X}	12.96	7.78

The most important finding, besides satisfactory yield already discussed, is the existence of considerable variation between and within species. It becomes, therefore, very important the selection of the proper Platanus species prior to plantation establishment. Furthermore it should be considered the existing variation in the level of provenance and tree to tree within provenance. For this purpose trials combining species provenance and families have been established in a number of sites, representing the major subdivision of the regions in Greece where Platanus can be cultivated, with irrigation or without irrigation. It also investigated the yield of plantations of 3 by 3 meters spacing and rotations from 9 to 10 years.

Maximization, however, of yield is anticipated to occur by using highly productive clones selected from our breeding programme. Clonal test will show which is the best clone or clones for each particular site. It seems, from the results obtained so far, that clones selected from families of P. occidentalis X P. orientalis hybridization are the most promising for our environments. The most important question, however, which should be answered is the behaviour of these clones under competition (multiclonal plantations) or without competition (density effect) in monoclonal plantations, of various spacings. Experimental data of other fast growing species, have shown that competitive ability is a character under genetic control which is independent from growth (Panetsos 1980 in press). Some clones grow very well under close spacing while others exhibit maximum growth in the absence of competition.

In conclusion it can be stated, from the results obtained, that Platanus species are

promising for short rotation forestry system in Greece. Yield can be considerably increased by planting in the right site the best genetically improved material and applying proper spacings and intensive cultural operations such as disk-ing, fertilizers, herbicides and in some cases irrigation. According to Steinbeck (1980) when American sycamore was grown in various rotations, energy inputs to energy outputs ranged from 1 to 17 and averaged 15,3 energy out:in.

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1. ENERGY VERSUS ECOLOGICAL CRISIS

Apart from the unquestionably accepted energy crisis we must not close our eyes to the ecological crisis. Attempts for the alleviation of the former are frequently considered radically erroneous by those who evaluate the latter as of primary importance. This controversy is well illustrated in the nuclear power stations issue.

Those who are earnestly involved in the pressing need for tackling the ecological crisis have recently begun to realise that it is sheer romanticism to deny facing problems inherent to economic development (as for instance the establishment of nuclear stations); instead, they should provide their alternative solution to the problem.

Today, the liquid fuel shortage has led to immense projects for the exploitation of several different energy sources. Since coal or energy plantations and not only nuclear power stations create serious ecological problems, the role of ecologists is proven considerably important. In case of coal, the problems arising are land destruction by surface mining, air pollution by SO_2 , increase of atmospheric CO_2 , etc. The solution of the energy plantation sort presents again several implications though fewer than with coal, such as arable land decrease, disadvantages innate to monocultures, replacement of natural ecosystems by agroecosystems etc.

The solutions of all these problems are not at hand and we should do better to develop new methods so that natural systems will both maintain maximal diversity and provide energy and resources. Therefore, the knowledge of the structure and function of natural ecosystems is crucial for their ecologically sound and economically profitable management. In other words, information gained by studying the system responses in perturbations will be used in a way to prevent man's exploitation beyond natural tolerance

limits.

In the present work and based on the above considerations we have constructed a model of energy and resources exploitation for the mediterranean-type natural ecosystems already proposed recently (Margaris, 1979; Margaris, in press). Furthermore, it is our belief that by following basic ecological theory no degradation will result; on the contrary it is highly probable that natural systems diversity will be enlarged.

2. INVESTIGATING MEDITERRANEAN-TYPE ECOSYSTEMS PERTURBATIONS

The peculiar mediterranean climate - characterized by the alternation of mild, wet winters with hot and dry summers - prevails not only in regions around the Mediterranean sea but also in California, Central Chile, S. and SW. Australia and Southern S. Africa. The combination of water shortage and high temperatures during summer favours the frequent fire burst out; it is for this reason that the mediterranean-type ecosystems is often characterized as fire-induced or fire-adapted (Shantz, 1947). As an example the fire frequency in chaparral of California and maquis of S. France is in the range of 1 per 20-30 years (Biswell, 1974; Trabaud, 1973).

Plants dominating all mediterranean-type ecosystems (m.t.e.) are equipped with adaptive strategies enabling their post-fire recovery (Arianoutsou, 1979; Biswell, 1974; Naveh, 1973). Thus, this perturbation and its surpassing are considered to be incorporated in the ecosystem information pool. Certainly, the intervention of human activities results in either higher or lower, than the optimum, fire frequency. In both cases the systems are degraded, and this is our point of focus, since it is only higher frequency which is largely considered as damage.

2.1. Higher frequency fires

Fires occurring with higher than the optimum frequency, in Greece, (average meantime 5-10 years) are set by shepherds (Papanastasis, 1976) who can thus exploit the herbaceous vegetation flourishing the first post-fire years as well as the tender resproutings of the woody plants, equally well eaten by sheep and goats.

It must be mentioned here that 95% of the nitrogen contained in the above ground biomass is removed from the ecosystem in fire's smoke (Arianoutsou, 1979) and in a lower percentage the other elements such as magnesium, potassium etc. The system is well adapted to the perturbations caused by fire; through nitrogen fixing plants this element can be incorporated in the soil from the atmosphere, thus alleviating the previous loss. However, if intense grazing follows, herbaceous plants and resproutings are either eaten or trampled - thus heavily damaged - and the whole system degraded because the otherwise efficient adaptive mechanism cannot further work. The degradation often results to the "Asphodel deserts", which are very common in Greece. There are systems of extremely low productivity; the above ground biomass cannot surpass 150 g.m^{-2} while in the initial non-degraded maquis ecosystems it reaches approximately 4 kg.m^{-2} at least.

2.2. Lower frequency fires

The ecosystem degradation caused by the combination of frequent fires and the subsequent overgrazing has led, particularly in Greece, to the consideration of fire as a catastrophic event always attributed to criminal actions. The result is a fire-exclusion policy undoubtedly leading as well to severe damages due to the following reasons:

- (1) As a consequence of fire-exclusion policy, biomass is accumulated in the ecosystem. Thus, when eventually fire bursts out, the high temperatures developed result in the damage of the recovery mechanisms which the system has evolved.

For example, extremely high temperatures inevitably damage the seeds of the seed bank.

- (2) In the fire-excluded systems the diversity is reduced in terms both of plant and animal species. An illustrative example is that of the "complete protection" project of Mountain Fynbos where species especially protected were virtually eliminated as a result of fire-exclusion (Bands, 1977).

3. PERTURBATIONS IN THE SERVICE OF ENERGY AND ORGANICS EXPLOITATION

It is mentioned above that fire is an inherent factor of the mediterranean-type ecosystems. As a consequence of the recognition of this fact prescribed burning (Biswell, 1974) is put into work in California and Australia (Vines, 1968). However, the technique of prescribed burning can essentially face only a part of the whole problem. With either prescribed or wild fires immense quantities both of energy and organics are lost. In Greece, at least 15,000 ha are burnt each year; the result is damage of properties, since fire attacks not only natural ecosystems, loss of valuable energy and organics, and expenses for the accomplishment of the fire-exclusion policy. However, the integral consideration of the fire problem and the shortage of energy, wood, paper and cattle-food in Greece can at the same time provide solutions and help in maintenance of natural ecosystems.

4. ECONOMIC PROFIT

In previous works we have theoretically estimated the possible profits in energy and organics provided by the rotating harvesting technique of the mediterranean-type ecosystems, in Greece (Margaris, 1979; Margaris, in press). On a theoretical basis, a year round harvesting of 4% of the Greek surface, that means 1/10 of the area covered by mediterranean-type vegetation, would provide $9.4 \times 10^{13} \text{ Kcal}$, what corresponds to over 80% of the total imports in oil; it must be pointed that nowadays Greece imports 100% of the liquid fuel needs. However, the above estimated percentage far exceeds the real one, because of the roughness of the land relief.

Approximately half of 40% of the Greek surface corresponds to maquis vegetation with biomass of about 60 tons.ha⁻¹. Maquis ecosystems can be divided into four classes according to the level of harvesting feasibility

Harvesting feasibility	Harvesting index	Maquis percentage	ha
high	I	15	3960
moderate	II	30	7920
low	III	20	5280
almost impossible	IV	35	9240

The above classes and percentages must be taken into account as rough estimations.

Undoubtedly, the land relief is a factor which complicates the estimation of the harvest cost. On the contrary, land ownership does not seem to create serious problems because over 70% of these areas are not private.

If we use an appropriate machine which harvests, cuts the material into small items (cheaps) and carries away the product (self-propelled harvester) then we can make the following rough estimations:

- (1) The harvest rate will be 4, 3 and 2 km.h⁻¹ for the harvesting indices I, II and III, respectively. The mean rate amounts 3 km.h⁻¹.
- (2) The maximal harvester opening reaches 3m. Thus, approximately 9,000 m² can be harvested per day providing 50 tons of dry biomass (60% of the fresh material).
- (3) Daily work of 8 hours will result in harvesting 400 tons of dry biomass. Consequently, the yearly production will arise to 400X320=128,000 tons, or 6X10¹¹ kcal.
- (4) The total harvestable area is 0.9X8X320=2,300 ha per year. In consequence, since every year only 1/10 of the total surface will be harvested one machine is adequate for 23,000 ha.
- (5) The harvesting cost per year will be:

(5.1)	2 machine drivers	24,000
(5.2)	2 workers	12,000
(5.3)	Including a 10% output of the capital investment of a 10 year working harvester	16,000
(5.4)	Fuels	14,000
(5.5)	Service expenses and spare parts of the harvester	16,000

Total	82,000
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- (6) The transport cost of one ton to a distance of 10 km is considered to be 2\$. Therefore, the total one will rise to 256,000\$.

In consequence, one ton of dry biomass in the storage center will cost 2.64\$. It is a remarkably low price especially when compared with those of energy plantations, where an approximate cost of 5\$ is considered quite satisfactory (Bene et al., 1978). Furthermore, the total estimated cost of our proposal is three times less than that of coal, which is used presently in Greece for electricity production; and that without taking into account the non-renewable nature of coal deposits.

5. ECOLOGICAL ADVANTAGE

It is mentioned above that the technique of prescribed burning is used both in Australia and in California in the management of mediterranean-type ecosystems. However, it must be taken into account that with this technique the natural ecosystems are successfully preserved but on the other hand immense quantities of energy and organics are lost; moreover, there is always the danger the fire become uncontrolled, with a probability of about 10%.

In comparison with energy plantations there are much more. First, the areas proposed for harvesting are not private, thus alleviating the problem of land use. Second, problems connected with monoculture techniques are non-existent. However, what is more important in our opinion, is the possible increase of the system diversity. Ten years after the initial harvesting there will coexist areas harvested before 1-10 years; so that different stages of the post-fire succession will be present in the same ecosystem. Furthermore, there is a possibility of 10! com-

binations, between different post-fire stages, which can be brought into contact. In this way, the roles, the organisms can play in the system, are multiplied with a subsequent possible increase of the total number of both plant and animal species in the post-harvest period.

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1. INTRODUCTION

Plant matter, the product of photosynthesis has received considerable attention as an alternative or supplemental energy source to fossil fuels. Photosynthesis, originally responsible for the ultimate deposition of fossil fuels, constitutes the only process by which massive amounts of solar energy are captured and stored today. It has been estimated that biosynthesis renews biomass with a yearly fixation of roughly 150 billion tons of carbon. This source of carbon represents about twenty times more energy than the total annual world energy consumption (Brink, 1976). Efficient conversion of a small fraction of biomass could thus provide a substantial source of energy.

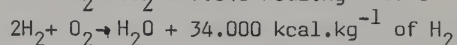
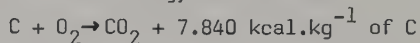
A number of processing methods—chemical, biological and thermolytic have been proposed whereby biomass may be converted to energy or fuels of higher utility. The thermolytic methods such as direct burning, pyrolysis and gasification, appear to be of more immediate interest. In the following the basics involved in the conversion of biomass into energy and energy chemicals with these methods are briefly discussed.

2. DIRECT COMBUSTION

Historically, biomass has served as the basis for energy production only to be displaced in the last century by coal. In turn the use of coal as our energy base has been displaced by petroleum. Biomass is still used extensively as a fuel for both domestic and industrial purposes and continues to play an important role in the energy economies of a number of countries (Pyle, 1979; Bethel, 1980). Today, as in the past, the most convenient way to use biomass for energy is to burn it for heat.

2.1. Fundamentals of biomass combustion, steam and electricity generation

Combustion is the rapid chemical combination of oxygen with the elements of fuel that will burn with the release of heat energy. The major combustible elements of lignocellulosic materials are carbon and hydrogen. Complete oxidation of these elements gives CO_2 , H_2O and heat energy as follows:



Taking the elementary composition of lignocellulosic material (carbon 50 \pm 2%, oxygen 40 \pm 3% and hydrogen 6.5 \pm 1%) the heat of combustion of biomass ranges from about 4,200 to 4,800 kcal per dry kilogram.

Table 1 gives a comparison of elementary analysis and heating values for wood, bark and some fossil fuels. The higher percentage of oxygen in the molecular structure of wood and bark gives them lower heating values as compared to coal and oil.

Woody materials have a substantial amount of water (moisture content M.C. % on a wet basis) which can vary from about 10 to 50% or more. Evaporation of the water requires energy which lowers the available heat of wood according to the equation (U.S.F.S. 1976):

$$\text{Available heat} = (\text{Oven dry heating Value}) \times \left(\frac{100 - \text{M.C.}\%}{100} \right)$$

Thus wood with an oven dry heating value of 4.500 kcal.kg $^{-1}$ and a M.C. of 50% has an available heat of 2.250 kcal.kg $^{-1}$.

Additional heat losses occur when wood is burned in industrial combustion furnaces. Table 2 gives the various sources of heat losses that occur in a boiler fired with hardwoods.

The amount of green wood required to generate 1 BoHP of steam (boiler horsepower = 8442 kcal.hr $^{-1}$) assuming a M.C. of wood 42% which gives an available heat of 2,525 Kcal.kg $^{-1}$ and a boiler efficiency of 63% (Table 3) is 5.3 kg.

The amount of green wood required to generate 1 kWhr

TABLE 1. Ultimate analyses and heating values of some fossil fuels compared with hardwoods.

	<u>Hardwood</u>				Residual
	Wood	Bark			fuel oil
<hr/>					
----- Percent -----					
Ultimate analysis					
Hydrogen	6.4	6.0	6.4 - 5.0		9.5 - 12.0
Carbon	50.8	51.2	54.6 - 74.2		86.5 - 90.2
Oxygen	41.8	37.9	33.8 - 17.1		-
Sulfur	-	-	.4 - 2.1		.7 - 3.5
Nitrogen	.4	.4	1.0 - 1.5		.01- .50
Ash	.9	5.2	3.3 - 10.1		
Heating value					
(kcal.kg ⁻¹)	4351	4222	5237	7400	9,680 - 10,560

TABLE 2. Overall boiler efficiency versus pine-site hardwood moisture content (Kasohesy and Kach, 1979).

Heat loss from	Moisture content			
	10%	25%	42%	50%
----- Percent loss -----				
H ₂ O in wood	1	5	12	16
H ₂ O from hydrogen in fuel	9	9	9	9
Dry stack gases	12	12	12	12
Incomplete combustion, radiation e.t.c.	<u>4</u>	<u>4</u>	<u>4</u>	<u>4</u>
Total heat loss	26	30	37	41
Overall boiler efficiency	74%	70%	63%	59%

(860,4 kcal) assuming the above conditions for wood and boiler and a 25% conversion efficiency from steam to electricity is 1,35 kg. Then, the

amount of wood required to fuel electrical generating plans are as follows (Karchesy and Koch, 1979):

Electrical Generating Plant Size	Amount of green hardwood required for fuel
5 MW	6.8 tons.hr ⁻¹
25 MW	34 tons.hr ⁻¹
250 MW	340 tons.hr ⁻¹
500 MW	680 tons.hr ⁻¹

2.2. Technical Processes

There are several industrial wood-burning systems available which, could basically fall into two classes of furnace design - the grate burners and the suspension burners. Within these two classes of furnace design there is a variety of furnace types which can differ markedly in basic operation, designed to accommodate the various forms of

fuel wood or other lignocellulosic materials. A more detailed description of the most important burning systems is given by Koch (1972), Karchesy and Koch (1979) and U.S.F.S. (1976).

Wood burning furnaces are commonly incorporated into boiler systems to produce steam. There are about 3,000 such wood fired boiler systems in operation in the U.S.A and Canada (U.S.F.S., 1976; Love and Overend, 1978). They range in size from shop-fabricated units with steam capacities up to 4,500 kg per hour to large field-erected units that can generate up to 300,000 kg of steam per hour. Most of the steam is converted directly to mechanical power or used for heat. Some boilers are incorporated into electrical plants to generate electricity. It has been estimated (Karchesy and Koch, 1979) that the generating capacity of existing electrical plants using wood or wood derived fuels in U.S.A. is about 4,500 MW. Recent studies in U.S.A. and Canada have shown that prospects for generation of electricity from wood wastes on a large-scale are quite optimistic.

In some furnace systems the hot combustion gases produced are used to direct-fire kilns and dryers without the intermediate step of steam generation (Koch, 1972). In addition, certain furnaces are used to drive gas turbines and their exhaust heat is used in a conventional boiler to produce added steam power (Kassat, 1979).

Much of the wood fuel is burned in fireplaces and domestic stoves (Lew, 1978; Pyle, 1979). Conversion efficiencies are low, ranging from 5-20% in fireplaces and from 10-70% in stoves, depending on their design.

In the Mediterranean countries fuel wood has

played an important role in their energy economies and has substantially contributed to their development. Almost all woody plants, trees, shrubs, dwarf shrubs and phrygana have been used for supplying domestic heat, for cooking and baking, particularly in rural areas. In Greece, more than 50% of the harvested wood volume is used today as fuelwood. Hardwoods, particularly Quercus comferta, Quercus coccifera and Fagus species are the main sources of fuel wood in northern Greece. Conifers such as Pinus halepensis, Pinus brutia and Abies chephalonica are the main sources of fuel woods in southern Greece. Rich in oleoresin old stumps of Pinus halepensis trees are still being collected and used for starting the fire in fireplaces, stoves and bakeries. In many villages of Greece, various species of phrygana have been used for heating old type furnaces for baking bread. Paliurus australis is the main species used for this purpose in northern Greece. A small number of steam generating plants continue to exist in Greece. Most of them are used by the forest products industries and are fueled with wood manufacturing residues, such as sawdust and bark.

3. PYROLYSIS

The pyrolysis of lignocellulosic materials refers to thermal degradation resulting in char, liquids and gaseous products (Fig. 1). Processes for the thermal decomposition of carbonaceous material are variously described as pyrolysis, liquefaction, carbonization, distillation, destructive distillation, gasification and thermolysis (Nikitin, 1966; Wenzl, 1970). Some of these terms are synonymous, but all involve the production of gaseous, liquid and solid products, albeit in different amounts depending on reaction conditions. In its strictest definition, pyrolysis is carried out in the absence of air, although pyrolysis has more recently found broader definition in describing any chemical changes brought about by the application of heat even with air or other additives (Soltes, 1978).

Pyrolysis can be best defined (Brink et al, 1976) as the destructive distillation of organic materials heated up to about 600°C without the addition of

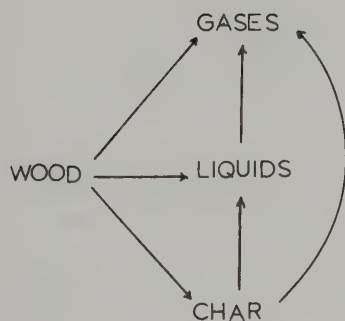


FIGURE 1. Products of wood pyrolysis

oxygen. Rate of temperature change, residence time and composition of materials introduced into the reactor determines the nature of the products formed. With a slow temperature change, decomposition of organic matter proceeds in an orderly arrangement, forming increasingly stable

molecules, richer in carbon. Charcoal becomes the primary product. Very rapid heating or "flash" pyrolysis produces char and relatively long chain hydrocarbon gasses that if not subject to further thermal degradation can be condensed into liquids. Pyrolytic oil becomes the primary product. Complete gasification on the other hand occurs as the products of pyrolysis are heated from 600°C to around 1000°C. Pyrolysis of woody materials yields char, noncondensable gases, and condensable vapors. The condensable vapors yield crude pyroligneous acid, soluble and insoluble tars (Table 3). Tars are a mixture of a large number of chemical compounds mainly phenolic in nature. Pyroligneous acid contains at least 60 compounds, the most important being methanol and acetic acid. The elemental composition of charcoal, the exact composition of tar, of pyroligneous acid and of gasses, and the yields of the individual products are a function of the reaction conditions employed and the chemical composition of the materials

TABLE 3. Yields of products of thermal decomposition of wood. (Final temperature 400°C; duration of heating 8 hours).

Products	Yields of products, %		
	birch	pine	spruce
Carbon	33.66	36.40	37.43
Pyroligneous distillate:			
settled tar	10.42	10.81	10.19
soluble tar	3.75	5.90	5.13
volatile acids (calculated as acetic acid)	7.66	3.70	3.95
alcolols (calculated as methanol)	1.83	0.89	0.88
aldehydes (calculated as formaldehyde)	0.50	0.19	0.22
esters (calculated as methyl acetate)	1.63	1.22	1.30
ketones (calculated as acetone)	1.13	0.26	0.29
water	21.42	22.61	23.44
Total	48.31	45.58	45.40
Gases:			
carbon dioxide	11.19	11.17	10.95
carbon monoxide	4.12	4.10	4.07
methane	1.51	1.49	1.59
ethylene	0.21	0.14	0.15
hydrogen	0.03	0.03	0.04
Total	17.06	16.93	16.79
Losses (by difference)	0.94	1.09	0.38

(Nikitin, 1966)

being pyrolyzed (Nikitin, 1966; Wenzl, 1970). Table 4 gives the elemental composition and yield of woodcharcoal as a temperature function.

3.1. Chemical Products of Wood Pyrolysis

Pyrolysis of wood was probably man's first chemical process (Soltes, 1978). Destructive distillation is known to have been made by the ancient Chinese. The Egyptians, Greeks and Romans made charcoal by wood carbonization and collected the condensable volatiles for embalming purposes and for filling joints in wood ships. Until the

quantities of methanol, acetic acid and acetone (Soltes, 1978). In the period of 1950-1965, acetic acid was produced from wood distillation in U.S.A at a rate of about 10 million kg per year (Klapproth, 1977). In the period from 1966 to 1976, methanol was produced from wood distillation in U.S.A. at a rate of about 5 million kg per year (Blackford, 1977). Destructive distillation of resinous wood was once of great economic importance in the manufacture of naval stores (Koch, 1972). The principal raw material for this industry was resinous heartwood from pine trees, logs and stumps. The destructive distilla-

TABLE 4. Elementary composition and yield of charcoal in relation to the carbonization temperature (Wenzl, 1970).

Carbonization temperature ($^{\circ}\text{C}$)	Elementary composition (%)			Yield (%)
	C	H	O	
200	52,3	6,3	41,4	91,8
300	73,2	4,9	21,9	51,4
400	82,7	3,8	13,5	37,8
500	89,6	3,1	6,7	33,0
600	92,6	2,6	5,2	31,0
800	95,8	1,0	3,3	26,7
1000	96,6	0,5	2,9	26,5

late 1800's wood carbonization was the major pyrolysis process and supplied the increasing amounts of charcoal that were required for iron ore smelting and for domestic fuel. Charcoal was also used to pack meat and make printer's ink, black paint and medicines (Youngquist and Fleisher, 1977). At the same time, increasing amounts of methanol (wood alcohol) were needed in a growing intermediate dye and synthetic organic chemicals industry. Methanol was being distilled from hardwoods in processes which recovered the volatile fraction of wood pyrolysis. The vapors produced were condensed to give a tar and the aqueous pyroligneous acid. Further processing of pyroligneous acid produced methanol and acetic acid. Wood gas was scrubbed and used for fuel. By the turn of the century, wood was the only source for bulk

tion process for pine was similar to that used for hardwoods, except that the products were charcoal, turpentine, dipentene, pine oil, pine tar, tar oils and pitch. Pine yielded less methanol and acetic acid and there were rarely recovered. Today the production of acetone, acetic acid and methanol from wood distillation is rarely economically attractive in the west Hemisphere. Russia, and other Soviet Block countries, however, continue to use wood for chemicals through distillation. Much of the rest of the world still relies on wood carbonization to yield charcoal, while chemicals are only occasionally produced as byproducts (Soltes, 1980). Charcoal represents the largest component in wood pyrolysis products (Table 3). Depending on its elemental analysis and other properties charcoal finds today application in a number of uses.

Table 5 (Wenzl, 1970) lists 5 domestic and specialized fuel applications, 9 metallurgical and 15 chemical uses for wood charcoal.

liquid and gaseous products. As a process, pyrolysis is flexible in the relative yields of these products and it can be used on a variety of biomass raw mate-

TABLE 5. Commercial application of charcoal (Wenzl, 1970).

Domestic and specialized fuel	Metallurgical	Chemical
Recreational	Copper	Carbon disulfide
Curing tobacco	Brass	Calcium carbide
Cooking in dining cars and in restaurants	Pig iron	Silicon carbide
Heating, foundry, plumbing equipment	Steel	Sodium cyanide
Heating in shipyards and citrus groves	Nickel	Potassium cyanide
	Aluminum	Carbon monoxide
	Electro manganese	Activated carbon
	Armor plate	Black powder
	Foundry molds	Fireworks
		Rubber
		Gas adsorbent
		Crayons
		Soil conditioner
		Pharmaceuticals
		Poultry and animal feeds

Wood tars also have a number of applications today (Wenzl, 1970). Sedimentation tar is first fractionated into tar oils and tar pitch. The pitch can be used as a cement and embending agent. The tar oils are further fractionated into light, heavy and high boiling oils and used as a flotation and impregnation medium or as fuels. A phenolic fraction is used as an effective antioxidant or cracking inhibitor for gasoline. Phenols are probably the most valuable product of wood pyrolysis. Wood tars, because of their high phenolic content (Table 6) have received much attention recently, particularly in Russia. Attempts to isolate single reactive phenols have been numerous and technical feasibility has been generally established in many cases (Soltes, 1980).

3.2. Pyrolysis Fuels

By definition pyrolysis of biomass produces solid

rials.

Charcoal, the solid product of pyrolysis, depending on its elemental composition (Table 4) has a heating value of about 5,500 to 8,000 kcal.kg⁻¹ which is comparable to that of a high grade coal or a low grade fossil oil (Table 1). Thus charcoal is a superior fuel to wood in that more than half the caloric content of wood is processed into a high grade fuel. In comparison to coal woodcharcoal has a low moisture and a negligible sulfur content. Charcoal can be used either for direct burning or converted further to liquid or gaseous fuels. For these reasons, it has been suggested (White, 1978) that in energy usage biomass be first converted into charcoal. Considerable effort in pyrolysing biomass to energy fuels has been concentrated recently on the production of a high caloric content pyrolytic oil. Knight and Bowen (1975) describe a steady - flow pyrolysis system (Tech-Air system) that produces in addition

TABLE 6. Yield and properties of oils obtained from the pyrolysis of various wood species (Wenzl, 1970)

Wood species and type of pyrolysis	Tar oil (%)	Phenol in tar oil (%)	Neutral substances (%)
Wood pyrolysis, technical	78.4	54.2	30.3
Logging waste, technical	57.3	63.2	31.3
Logging waste, experimental	66.0	56.0	36.0
Hardwood, dry distillation	86.5	42.0	52.0
Beechwood, dry distillation	57.8	50.0	33.0
Beechwood, vertical retort	64.6	35.0	24.7

to charcoal a pyrolytic oil with a heating value of 6,700-8,000 kcal.kg⁻¹ (Fig. 2). The oil is obtained by passing the pyrolysis vapors through a condenser. The remaining noncondensable gases are used to dry wood prior to processing. The oil

The pyrolytic oil produced has a heating value of about 6,000 kcal.kg⁻¹ and it is intended to be sold as substitute for No. 6 residual fuel oil (Table 8). The process was developed primarily for pyrolyzing municipal wastes while recovering valuable metals

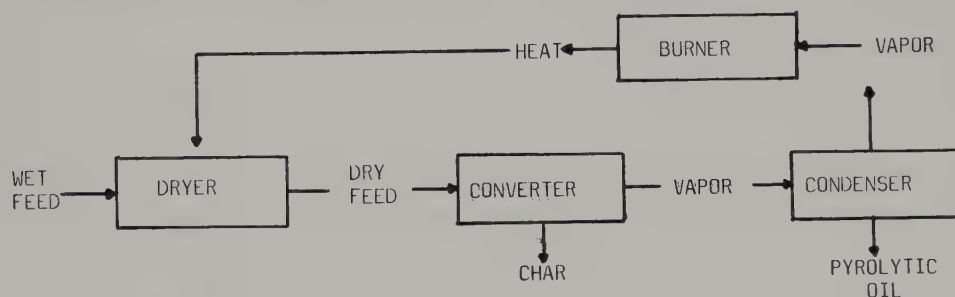


FIGURE 2. Flow diagram of the Tech-Air Pyrolysis system

and char products combine 70% of the input energy in 50% of the input dry weight. Table 7 (Knight, 1976) gives heating values of pine-sawdust pyrolytic products at various conversion temperatures. The Tech-Air system is designed to convert various forms of agricultural and forestry wastes. Preston (1976) describes a pyrolysis system (Occidental Flash Pyrolysis) that is aimed at producing a maximum yield of combustible oil. The charcoal produced is recycled internally in the system in order to supply heat energy for the pyrolysis process. The pyrolysis gases having a heating value of about 3,500 kcal.m⁻³ are also recycled and used for process heat requirements.

and glasses, but is equally suitable for woody materials (Pober and Bauer, 1977). Typical yield products of the processes are: 40% oil from municipal solid waste, 30-45% oil from rice hulls, grass straw and Douglas-fir bark.

Liquefaction (Lindemuth, 1978; Malton et al., 1978; Krames, 1980) is another process which has been proposed to convert biomass to liquid fuel (Fig. 3). Biomass is converted to an oil by reaction with synthesis gas and an alkaline catalyst (sodium carbonate) under high temperature and pressure. Part of the biomass can be used to produce the synthesis gas by gasification. Maximum conversion efficiency from wood was 58% and the resulting oil had

TABLE 7. Typical properties of No. 6 fuel oil and pyrolytic oil (After Preston, 1976)

	No. 6 <u>Fuel Oil</u>	Occidental <u>Pyrolytic Oil</u>
C, wt. %	85.7	57.0
H	10.5	7.7
S	0.7-3.5	0.2
Cl	-	0.3
Ash	0.05	0.5
N	-	1.1
O	2.0	33.2
Density, g.ml ⁻¹	0.98	1.30
kcal.kg ⁻¹	10,120	5.892
kcal.liter ⁻¹	39,360	30,360
Pour point, °C	18-29	32
Flash point, °C	66	56
Viscosity	360	1150
SSU at 190 F	46	71
Pumping temperature, °C	105	116
Atomization temperature, °C		

TABLE 8. Heating Values of Pyrolytic Products (After Knight, 1976)

Product	Furnace temperature			
	540°C	650°C	700°C	870°C
Gas (kcal.m ⁻³)	3098	3223	3517	3642
oil, first condensate (kcal.kg ⁻¹)	7520	7822	7312	7024
oil, second condensate (kcal.kg ⁻¹)	6758	7535	7024	7069
oil, dry ice condensate (kcal.kg ⁻¹)	7428	7584	7388	7467
Char (kcal.kg ⁻¹)	7981	8028	7904	7812

the properties shown on Table 9. On a volume basis, four times higher than that of wood. the heating value of wood-produced oil is about

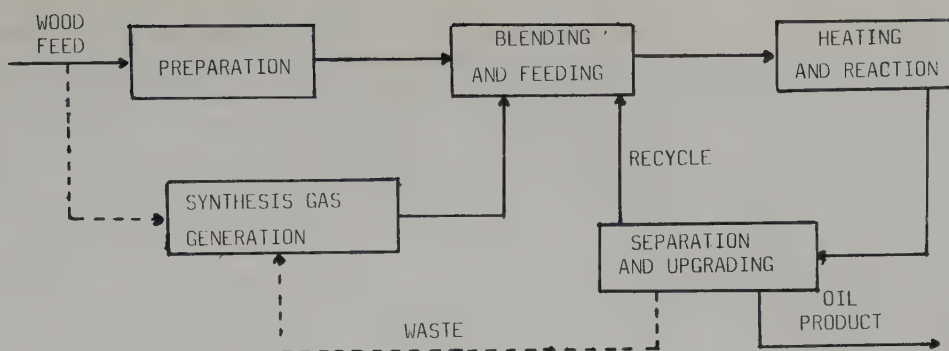


FIGURE 3. Flow diagram of a liquefaction process (Lindemuth, 1978)

TABLE 9. Average properties of wood produced oil (Lindemuth, 1978; Krames, 1980)

	Reactor residence time	
	20 min	60min
Density g.cm ⁻¹	1.05 - 1.10	
Viscosity CP	200 - 1000	
Heating value kcal.kg ⁻¹	8730 - 8895	
Elemental analysis		
% C	86.0	88.3
% H	6.4	6.7
% O	6.4	4.0
% N	0.4	0.1

4. GASIFICATION

Gasification is the thermal decomposition of organic materials in the presence of controlled and limited amounts of oxygen to produce a combustible mixture of gases, often referred to as "producer gas". When air is used, the produced gas contains mostly hydrogen, carbon monoxide and nitrogen. The mixture having a heat value from 900 to 1800 kcal.m⁻³ is generally referred to as a low calorie gas. When oxygen is used for gasification medium calorie gas with heating values as high as 3500 kcal.m⁻³ is produced. Nitrogen dilution is eliminated so that the two major components of medium calorie gas are hydrogen and carbon monoxide. Lesser amounts of

carbon dioxide, methane and hydrocarbons are also produced in both cases (Table 10). The exact chemical composition of either low or medium calorie gas depends on variables that include temperature, pressure, time and presence of catalyst (Love and Overend, 1978). The basic processes in gasification are similar to those in combustion except that complete oxidation of carbon and hydrogen to carbon dioxide and water, respectively, is avoided. The primary objective of the gasification processes is the quantitative conversion of lignocellulosic or other carbonaceous materials to gaseous products that can be further used either as fuel or as a raw material in the production of chemicals (Fig. 4).

Wood gasification has been commercially practiced

TABLE 10. Typical composition for low and medium calorie gases produced on gasification of biomass

	Low calorie gas	Medium calorie gas
	Percent	
Carbon monoxide (CO)	20	40
Hydrogen (H ₂)	15	30
Carbon dioxide (CO ₂)	10	20
Hydrocarbons (CH _x)	5	10
Nitrogen (N ₂)	60	-

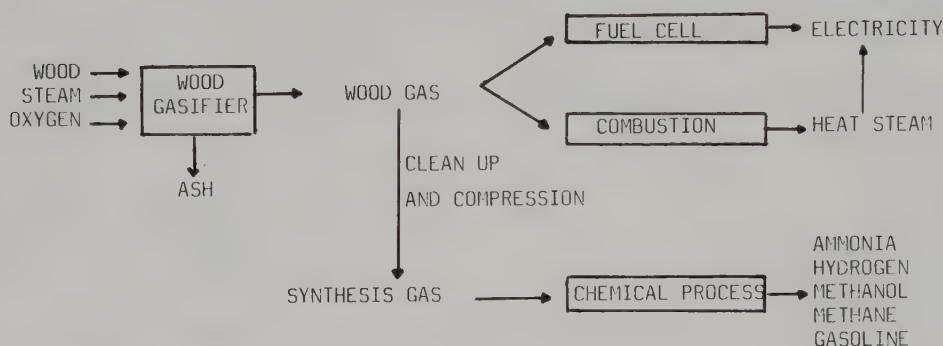


FIGURE 4. Gasification scheme for the production of energy and chemicals.

for at least 120 years (Amundsen, 1976). Early gasification units operated by blowing air up through a fuel bed and allowing gases to exit the top of the gasifier. The producer gas was used directly to fire boilers and furnaces or after cooling and cleaning to fuel internal combustion engines (Levelton and O'Connor, 1978). Portable gasification units were developed before and during World War II. In Europe during World War II, about 700,000 vehicles were adapted to use producer gas from coal, charcoal, wood and crop residues (Levelton and O'Connor, 1978; Papaioannou, 1960). Wood gas was also used to produce alcohols and other hydrocarbons by the Fischer-Tropsch method before and during the second world war. In 1935 about 4,000 automobiles in 11 countries were fueled with alcohol produced from wood gas (Gasche, 1978).

Renewed interest has aroused recently on gasification for converting biomass to energy of energy chemicals and many types of wood gasifiers exist or are in various stages of development (Brink, 1976; Farfarman 1976; Hokanson and Rowell, 1977; Horsfield, 1976; Levelton and O'Connor, 1978; Valey, 1976; Voss and Ganger, 1977). Most of the gasifiers are air blown and produce a low calorie gas suitable to be burnt on site so that the sensible heat of the gas can be utilized. Such on site utilization is best for low calorie gas since the gas cannot be stored effectively and its low heat content makes transport economically unattractive.

Recent studies (Goldstein, 1979; Hokanson and Rowell, 1977; Pyle, 1979; U.S.D.F., 1976) have examined the possibilities of using biomass gas as synthesis gas for methanol production. Gasification systems, purification requirements, shift reaction needs, mate-

rial balances, plant sizing and estimates of investments were examined. They concluded that production of methanol from wood wastes is technically feasible. The work of Intergroup Consulting Economists Ltd (Pyle, 1979) showed that the prospects for large-scale sophisticated fuel production from wood are concluded to be good.

Prahaes et al. (1971) have evaluated gasification processes of converting wood wastes to methanol or ammonia and arrived at favourable conclusions concerning the feasibility of such processes. Farfarman (1976) and Scheider (1976) have investigated the possibilities of harvesting, transporting and gasifying chaparral to methane. Anderson (1978) and Meisel et al. (1976) have shown that gasohol can be produced from wood or other lignocellulosic materials (Fig. 5).

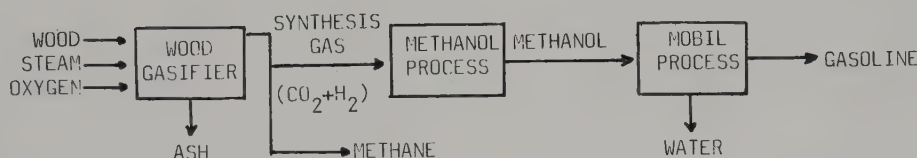


FIGURE 5. Scheme for the production of gasoline from wood.

4.1. Concluding Remarks

As the search for alternatives to petroleum fuels is pursued, biomass is commonly lumped with the so called "unconventional sources" though clearly it is not an exotic new source of energy whose use must await the creation of new technology. Biomass can be converted to energy in a number of ways.

Direct combustion of biomass, is the age old process with which man has supplied energy needs throughout his existence. A vast array of organic materials have been used. Wood particularly, but also bark and grasses, have dominated plant matter from other sources for use in furnaces and boilers. Still today, use of plant matter is considered a viable alternative to fossil fuels for generation of power. The technology for its

use has been modernized and automated. Under some circumstances wood fuel has been competitive with oil and natural gas. As cost of the fossil fuels are increased, the use of wood fuel should become increasingly attractive.

Pyrolysis and gasification technologies are being developed as alternatives to direct burning for the generation of energy from organic matter. These technologies have the added advantage of production of an improved fuel that can be used in numerous ways other than generation of steam power.

As an energy source, biomass has a number of advantages as compared to fossil fuels. It can be used as fuel in solid, liquid or gaseous form. It burns without significant toxic emissions. It is widely distributed geographically. It maintains products options. It provides a convenient way of storing

energy for future uses. Moreover, it is renewable. To biomass as a fuel it has been also assigned some disadvantages: It has a heat value to weight ratio when compared with some fossil fuels. It has a substantial moisture content as it comes from the forest or crops. Geographical desparation of biomass makes collection and transportation expensive. These disadvantages could be at least partially offset by using biomass on site or by converting it to higher densities - higher energy solids (char) or liquids (pyrolytic oil or methanol). In addition, technologies are being developed for harvesting and densifying biomass into pellets which can be easily and economically transported.

Mediterranean vegetation has served its people as a source of energy since the very ancient times and has contributed thus substantially to the development

of civilization in this area. Although, this long and most irrational use of wood and other plant materials for meeting the energy or other needs of the people has had some undesirable effects too, mediterranean ecosystems can still play a vital role for securing energy from their biomass, provided that their productivity is increased, and modern technology in converting biomass into energy applied.

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PART FIVE

PLANT AND STAND ENVIRONMENT

The mediterranean-climate regions of the world have distinctive climates and vegetation structural characteristics. The climate is defined by cool, wet winters and warm, dry summers. The vegetation is defined by the predominance of hard-leaved, evergreen shrubs. These definitions are in terms of typical and mean conditions. Deviations from the mean climatic conditions occur because of day to day variations, because of different exposures of the land surface, and because of the influence of the vegetation canopy on processes of energy exchange and microclimate. These deviations can be critical to the germination of seeds and survival of seedling.

Climates and microclimates depend on solar energy first and foremost. Solar energy warms plants and other surfaces, which in turn warms the air, generates winds, and evaporates liquid water. It is obviously important in photosynthesis. In spite of its general importance, data on solar irradiance in a given locality as well as comparative syntheses of data between regions are scarce. A comparison of mediterranean-climate regions in different latitudes and different hemispheres should include a characterization of solar irradiance.

Correlations of the distribution of species and vegetation types with air temperature and precipitation provide broad introductory frameworks within which the causal mechanism of the environmental control of plant growth and vegetation development can be studied. Plant species in mediterranean-type climates must survive two periods and types of stress-winter cold and summer drought. While the summer drought is part of the definition of mediterranean climate, the winter cold of particular importance to plant survival may be the deviation from the typical, mean conditions. The summer drought will vary from year to year in its length, but not usually in its intensity; i.e., in the climatic regime of 300 to 700 mm yr⁻¹ soils become dry every summer. The intensity of winter cold and the length of summer drought depend on topographic and soil conditions. The topography of mediterranean-climate regions is typically heterogeneous and steep. The different exposures through their influence on solar irradiance develop different micro-environmental conditions. The microenvironmental conditions include different soil surface temperatures and rates of surface soil drying, both of which are important in the establishment of young plants. The observed difference in vegetation of surfaces of different exposures is due partly to the different microenvironmental conditions and species responses can be explained on the basis of the physical processes of energy exchange, of which characterization of solar irradiance is a first important step.

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LOW TEMPERATURE EFFECTS ON MEDITERRANEAN SCLEROPHYLLS: AN UNCONVENTIONAL VIEWPOINT

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1. INTRODUCTION

Mediterranean sclerophyllous trees and shrubs are considered to represent a life form which, by evolution and natural selection, has adapted to climates with summer drought and wet, mild winters. Obviously drought stress proves to be the climatic factor essentially responsible for the restriction of productivity, growth, and survival of evergreen woody plants in Mediterranean-type regions. In addition, low temperature effects in marginal districts, particularly in the northern and eastern parts of the Mediterranean basin and near to the altitudinal limit of the maquis vegetation, should not be neglected. Such effects are frost damage during severe winters, which are to be expected every 10 - 12 years (Morettini 1961), as well

as reduced dry matter production and decreased vigour of the plants due to the depression of metabolic activities by suboptimal temperatures in December and January (Killian 1933, Larcher 1961a,b, 1969a,b, Eckardt et al. 1975, Weinmann, Kreeb 1975). Recently the significance of low winter temperatures and episodic frost in limiting distribution range and causing alterations in the floristic composition of the maquis vegetation in Europe has been emphasized by Larcher (1980a) and Mitrakos (1980). Experimental data from previous investigations are evaluated here to illustrate the view that low temperatures, which were a major stress factor during Pleistocene, still exert a considerable influence on survival, reproduction and productivity of Mediterranean evergreen woody plants.

TABLE 1. Frost resistance of vegetative organs of adult specimens of Mediterranean sclerophylls and conifers in December and January. Data indicate temperatures ($^{\circ}\text{C}$) which cause 50% injury (from Larcher, Mair 1969, Larcher 1970).

Species	Leaves	Leaf buds	Stem cambium	Stem xylem	Root cambium	Root xylem
<i>Ceratonia siliqua</i>	-6	-8	-9	-11		
<i>Nerium oleander</i>	-8	-12	-14	-15		
<i>Myrtus communis</i>	-8	-11	-17	-15		
<i>Laurus nobilis</i>	-12	-10	-14	-16	-6	-7
<i>Olea europaea</i>	-12	-13	-20	-18		
<i>Quercus cocciifera</i>	-12	-13	-21	-22		
<i>Quercus suber</i>	-11	-16	-26	-22		
<i>Arbutus unedo</i>	-12	-17	-18	-16		
<i>Rhamnus alaternus</i>	-12	-18	-17	-16		
<i>Viburnum tinus</i>	-13	-15	-20	-17		
<i>Pistacia lentiscus</i>	-14	-16	-20	-17		
<i>Quercus ilex</i>	-15	-17	-28	-26	-7	-8
<i>Phillyrea latifolia</i>	-16	-20	-23	-22		
<i>Pinus pinea</i>	-13	-16	-19	-17		
<i>Pinus halepensis</i>	-13		-22	-18		
<i>Cupressus sempervirens</i>	-16		-29	-22		

2. LIMITATION OF THE DISTRIBUTION RANGE OF MEDITERRANEAN SCLEROPHYLLS BY WINTER FROST

During episodic winter frost, minimum temperatures of -10 to -12°C are observed near the northern and eastern limits of the Mediterranean region, and temperatures down to -6°C have repeatedly been measured in the western and central parts of this region. Such temperatures cause striking damage to evergreen trees and shrubs, and have been described in numerous publications. (for reference see Larcher 1954, 1963a). Frost events clearly demonstrate the inadequate resistance of Mediterranean sclerophylls to the lowest temperatures which may recur in their natural habitats. However, it is not easy to deduce specific limits of frost resistance from such reports, since in most cases the exact plant temperature during frost has not been measured and microclimate differs considerably from standard meteorological data. On the other hand, only few experimental investigations have been made on the frost resistance of Mediterranean sclerophylls (Larcher 1954, 1963b, 1969c, 1970, Larcher, Mair 1969, Sakai 1978). Freezing tests offer the best approach for obtaining reproducible quantitative data on frost resistance and, in addition, for studying the physiological events of frost killing and the mechanisms of frost resistance. If appropriately interpreted, the experimental data agree well with observations after freezing under field conditions (for comparisons see Larcher 1963a, Lavagne, Muotte 1971).

A selection of the data obtained from freezing tests is presented in table 1. Three groups can be distinguished with regard to frost susceptibility: *Ceratonia siliqua*, *Nerium oleander*, and *Myrtus communis* are the most sensitive species with 50% frost injury to the leaves at -6 to -8°C and to the shoots at -9 to -15°C . Observations after frost damage show that full recovery can not more be expected after 50% injury to the stem cambium and/or the xylem (Larcher 1963a,

TABLE 2. Frost resistance of reproductive organs of Mediterranean sclerophyllous plants in January: B = Flower primordia in winter buds; F = Opening flower buds and flowers; S = Seeds and fruits. From Larcher (1954, 1970).

Species	50% injury at $^{\circ}\text{C}$
<i>Laurus nobilis</i>	-7 (F)
<i>Laurus nobilis</i>	-7 (S)
<i>Rhamnus alaternus</i>	-8 (F)
<i>Viburnum tinus</i>	-8 (S)
<i>Viburnum tinus</i>	-10 (F)
<i>Quercus coccifera</i>	-12 (B)
<i>Quercus suber</i>	-14 (B)
<i>Quercus ilex</i>	-15 (B)
<i>Phillyrea latifolia</i>	-15 (B)

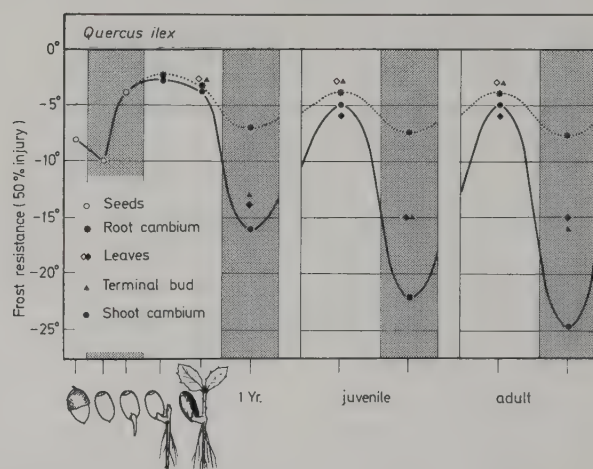


FIGURE 1. Frost resistance of *Quercus ilex* during germination, seedling establishment, and aging. Shaded areas: frost-hardened state in winter. From Larcher (1969c).

1981). The second group, which includes most of the Mediterranean woody plants such as *Laurus nobilis*, *Olea europaea*, *Quercus coccifera*, *Quercus suber*, *Arbutus unedo*, *Rhamnus alaternus*, *Viburnum tinus*, *Pistacia lentiscus*, and the Mediterranean conifers *Pinus pinea* and *P. halepensis*, shows serious damage to the foliage -12 to -14°C and to the stems at -15 to -20°C . The third group consists of particularly resistant species (*Quercus ilex*, *Phillyrea latifolia*, and *Cupressus sempervirens*), which are not seriously damaged until -15 to -25°C .

These groups reflect the latitudinal and altitudinal

gradients in the floristic composition of the maquis vegetation in the European mediterranean region, even if the presence of adult individuals are not necessarily indicative of the survival capacity of a species in a certain area. Indeed several Mediterranean sclerophylls can be cultivated far north of the proper climatic zone, provided the lowest temperatures are not below the specific resistance limit. The distribution area of a species is more likely to be determined by less resistant propagative organs and developmental stages such as overwintering flower buds (e.g. *Laurus nobilis*, *Rhamnus alaternus*, *Arbutus unedo*, *Viburnum tinus*) and immature fruits (e.g. *Laurus nobilis*, *Olea europaea*, *Arbutus unedo*) or germinating seeds and fast growing seedlings. The data listed in table 2 suggest that none of the Mediterranean sclerophylls would be able to produce flowers and fruits after a winter frost with tempera-

tures below -7 to -15°C . Particularly frost-susceptible stages are germinating seeds, seedlings, and young plants (Fig. 1). Mediterranean species germinate preferentially during autumn and winter, which are the wet seasons, favourable with respect to water availability but not necessarily as to temperature conditions. Thus the developmental stages most susceptible to frost are also the most endangered (Larcher 1973). As a consequence a frost of -5 to -10°C will destroy all the germinated seeds of that year, and if this occurs in successive winters, the propagation of the species becomes impossible (Larcher, Mair 1969).

3. LIMITATION OF CO_2 -UPTAKE OF SCLEROPHYLLOUS WOODY PLANTS BY SUBOPTIMAL TEMPERATURES DURING WINTER

Suboptimal temperatures result in increasing impairment of photosynthesis and, consequently, of dry matter production. The optimal temperature range for net photosynthesis of sclerophyllous plants

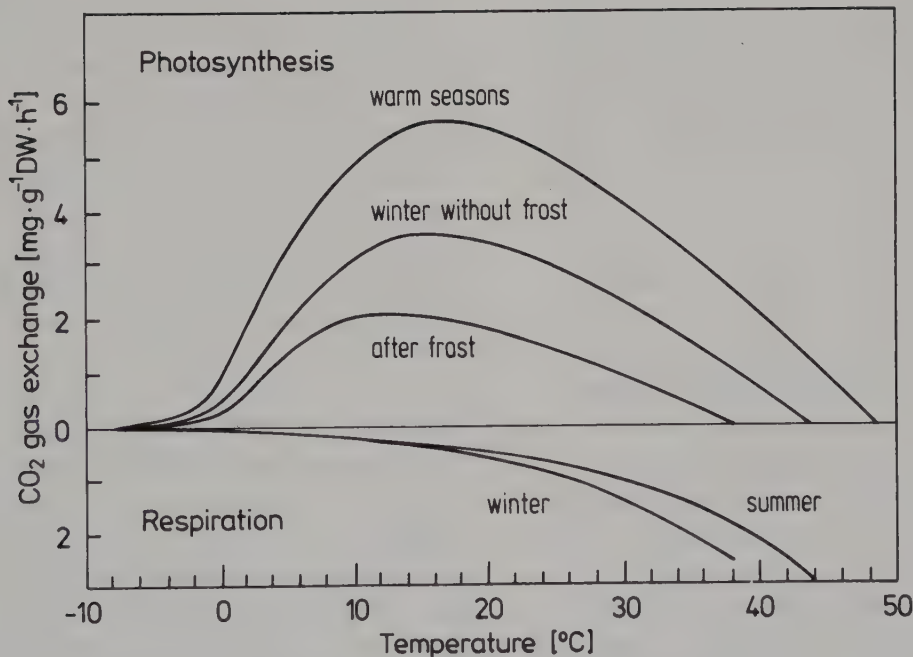


FIGURE 2. Temperature-dependent net photosynthesis and respiration of olive twigs at $40 \text{ W}\cdot\text{m}^{-2}$ irradiation ($177 \mu\text{mol m}^{-2} \text{ s}^{-1}$ photon flux density). From Larcher (1961a).

TABLE 3. Daylength at $\varphi = 40^\circ\text{N}$, and monthly means of daytime and night air temperatures at Herakleion (data from WMO 1971), Athenai (WMO 1971); Arco (Larcher 1979) and Bozen-Gries (Fliri 1975). The average temperatures during daytime (T_D) are calculated on the basis of the monthly means of daily minimum (T_{\min}) and maximum temperature (T_{\max}) according to the formula proposed by Milthorpe, Moorby (1979): $T_D = 0.5 (T_{\max} + T_{\min})/3$. Average night temperatures: $T_N = (T_{\max} + 3 T_{\min})$.

Location	Oct.	Nov.	Dec.	Jan.	Feb.	March	
Daylength at $\varphi 40^\circ\text{N}$	12.4	11.3	10.6	10.8	11.3	12.8	h.d^{-1}
Herakleion ($\varphi 35^\circ 20' \text{N}$, 38m a.s.l.)							
T_D	21.2	18.0	14.9	13.0	13.3	14.2	$^\circ\text{C}$
T_N	18.5	15.6	12.5	10.6	10.7	11.6	$^\circ\text{C}$
Athenai ($\varphi 37^\circ 58' \text{N}$, 74m a.s.l.)							
T_D	20.5	15.8	12.2	10.3	11.1	12.5	$^\circ\text{C}$
T_N	17.5	13.4	10.0	8.0	8.5	9.7	$^\circ\text{C}$
Arco ($\varphi 45^\circ 55' \text{N}$, 90m a.s.l.)							
T_D	15.2	9.6	6.3	4.8	6.6	9.8	$^\circ\text{C}$
T_N	12.8	7.6	4.6	2.9	4.6	7.8	$^\circ\text{C}$
Days with frost (average)	0	0.4	3	10	4	0.3	
Bozen ($\varphi 46^\circ 30' \text{N}$, 286m a.s.l.)							
T_D	13.8	7.2	2.6	1.7	5.0	10.1	$^\circ\text{C}$
T_N	9.8	3.9	-0.3	-1.2	1.6	6.2	$^\circ\text{C}$
Days with frost (average)	0	1	19	21	13	3	

of warm temperate climates lies between 15 and 35°C (Larcher 1980b); photosynthetic activity decreases significantly below 10°C . There are distinctive differences in the depression of CO_2 -uptake at suboptimal temperatures from one plant species to another: At 5°C *Olea europaea* attains approximately 50% and *Quercus ilex* 60% of maximum photosynthetic rates at optimum temperatures; at 0°C net photosynthesis of *Olea europaea* is restricted to 10% of the optimum rates and that of *Quercus ilex* to 25% (Larcher 1961a). Due to the property of persistent supercooling exhibited by sclerophyllous leaves, CO_2 -uptake can be maintained (at a very reduced rate $< 0.1 \text{mg.g}^{-1} \text{h}^{-1}$) even at negative temperatures (in winter until -4 to -8°C ; Larcher 1961a, Pisek et al. 1967, Weinmann, Kreeb 1975).

Besides the direct, instantaneous, influence of suboptimal temperatures on the reaction speed of metabolic processes there are also indirect, seasonal, environmental effects which result in lowering of the photosynthetic rates during win-

ter (see Fig. 2). In the Lake Garda region of Northern Italy, full activity is sustained until November, when air temperatures are 8 to 12°C by day and not below 5°C by night (see tab. 3). From December to February, when temperatures drop below 10°C during the day and night frosts (usually not lower than -3°C ; Larcher 1979) occur on more than 10% of all days, the *photosynthetic capacity* (i.e. the net photosynthesis peak rates at optimum temperatures) of *Olea europaea* achieves only 65%, that of *Quercus ilex* 75% of the summer and autumn capacity. During periods with frost every night, the photosynthetic capacity becomes depressed even further, i.e. in *Olea europaea* to 35% and in *Quercus ilex* to 60% of full capacity. At the same time, dark respiration is enhanced by a factor of 1.2 to 1.5. Winter depression of photosynthetic capacity has been reported for many evergreen woody plants (for references see Larcher 1969b, Kusumoto 1978), but the mechanisms of the induction processes are yet not fully understood. It is known that low temperatures and shorter day length trigger hormonal, biochemical, and

ultrastructural changes which lead to the various interdependent metabolic alterations, to cessation of growth and to an increase in cold resistance (e.g. Sosinska et al. 1977, Senser, Beck 1977, 1979, Martin et al. 1978).

The drop in carbon gain during winter depends on the local duration of suboptimal temperatures and the degree of the temperature decline, and on the specific metabolic sensitivity to low temperatures of the individual species. In order to illustrate the dependence of depression of CO_2 -uptake by suboptimal winter temperatures on local climate, the monthly sums of "estimated CO_2 -uptake" have been calculated for *Olea europaea*. The calculations are based on laboratory measurements of net photosynthesis rates using plant material from trees growing near Arco (shown in Fig. 2) and the monthly means of daytime and night temperatures (listed in Tab. 3). Similar estimates had already been made for 12 broadleaved evergreen species of Southern Japan by Kusumoto (1957, 1961) and for *Olea europaea* and *Quercus ilex* in Northern Italy (Larcher 1961b). In the present study the values of estimated CO_2 -uptake have been computed for a period of October through March for a series of selected localities within and immediately beyond the limits of the Mediterranean region. All calculations were made for an average latitude of 40°N and for local daytime temperatures. The localities chosen were: Herakleion, with particularly mild winter temperatures, Athenai with typical winter conditions for Southern Europe, Arco with winter temperatures characteristic of the northern limit of the distribution area of mediterranean sclerophylls, and Bozen with temperatures characteristic for habitats with submediterranean vegetation. At Herakleion, daytime temperatures are never below 13°C during winter, but average minimum temperatures may decrease to 9°C in January and February; the native sclerophyllous flora includes even very cold-sensitive species like

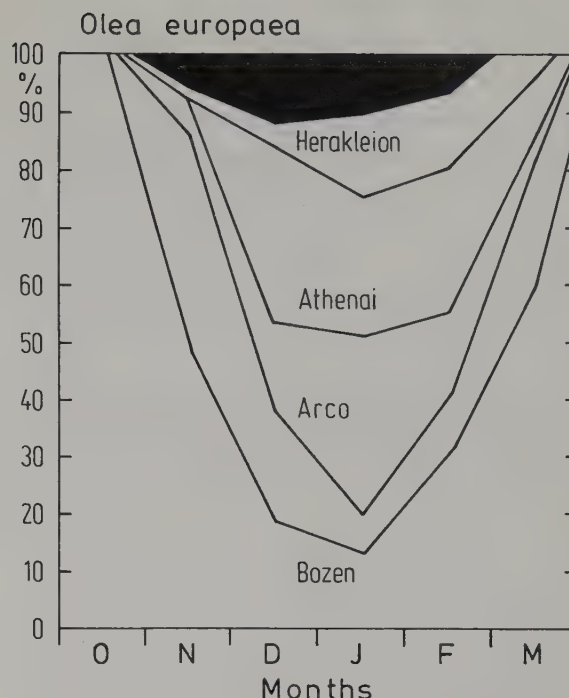


FIGURE 3. Estimated relative monthly CO_2 -uptake of olive twigs related to the temperature climate of selected locations with mediterranean and submediterranean climate, expressed as percentage of maximum CO_2 -uptake at optimum temperature and constant daylength of 12 hours. Shaded area: Effect of the variation of daylength at 40°N .

Ceratonia siliqua (Mitrakos 1980). At Athenai daytime temperatures remain above 10°C during the whole winter, average minimum temperatures are 6.5°C in January to March; maquis vegetation is well developed, but *Ceratonia siliqua* is missing. The Lake Garda region, where relicts of *Quercus ilex* woodland have been persevered and olive trees are cultivated, can be considered as an area that is still influenced by Mediterranean climate. There *Phillyrea latifolia* and *Rosmarinus officinalis* are probably native (Arietti 1965) and several other Mediterranean sclerophylls like *Nerium oleander*, *Laurus nobilis*, *Arbutus unedo* and *Viburnum tinus* have been introduced with success (Larcher 1979). At Arco the daytime temperatures are below 10°C from November to March, and are approximately 5°C in January. The night temperatures are below

5°C for the same period, and night frosts are fairly frequent during December, January and February. The winter climate in Bozen differs from that of Arco in the remarkably lower temperatures and higher frequency and longer duration of frosts. However, the absolute minimum temperatures are not much lower than -12°C, thus permitting the survival of adult Mediterranean sclerophylls of which some species are planted in parks and gardens.

In Fig. 3 the monthly "estimates of CO₂-uptake" are expressed as percentages of a hypothetical maximum uptake during 12 hours of daylight and at optimum temperatures for the net photosynthesis of *Olea europaea* ("maximum level"). The diminution of CO₂ gain due to variation of day-length in winter was calculated on the basis of monthly totals of daylight hours at a latitude of 40°N (see table 3) and a constant optimum temperature for CO₂-uptake of *Olea* ("optimum level"); the estimated cumulative CO₂-uptake during the short day period of October to March (11.41 g CO₂.g⁻¹ DW) is 4% lower than hypothetical maximum yield (11.88 g.g⁻¹), even though the temperatures remain within the optimum range. In the southern parts of the Mediterranean region and at low altitudes, where *Ceratonia siliqua* is a common component of the maquis vegetation, the estimated cumulative CO₂-uptake during the 6 months' period ("maquis climax temperature level" at Herakleion: 10.63 g.g⁻¹) is 11% below the hypothetical maximum level. The net effect of sub-optimal temperatures consists in 2/3 of the total yield depression at Herakleion. It may be of interest to paleo-ecology that, if ambient temperatures for positions on the Canary Islands at altitudes of 500-1000m are used (La Laguna and Aquamansa, Tenerife; Abreu 1977), nearly the same estimates of CO₂-uptake as for Herakleion are obtained. At these altitudes the climax vegetation are laurel woods, which are regarded as relicts of preglacial

Mediterranean forests (Ceballos, Ortuño 1951, Meusel 1965, Bramwell 1974, Sunding 1979). The estimate for 6 months' CO₂-uptake by *Olea europaea* subjected to a Macaronesian laurisilvae climate would amount to 10.95 g.g⁻¹, i.e. 92% of the cumulative maximum level. Beyond the distribution limit of *Ceratonia siliqua* in Greece (Athenai) the estimated cumulative CO₂-uptake of *Olea europaea* is only 74% of the maximum level (or 77% of the optimum and 82% of the climax level). In January at Athenai the estimated cumulative CO₂-uptake of *Olea* is only half the highest possible yield (see Fig. 3) or 70% of that at climax conditions. At the northernmost habitats of Mediterranean sclerophylls the six month's estimates are 7.39 g.g⁻¹ at Arco (i.e. 62% of the maximum level and 69% of the climax temperature level), and 5.51 g.g⁻¹ at Bozen (i.e. 46% of the maximum level and 52% of the climax temperature level).

Further investigations are needed to clarify whether certain depressions in photosynthetic yield, such as the value of 70% for the maquis climax temperature level (at Athenai during the coldest month, at Arco on the average for the whole winter), are of general applicability as a measure of critical suboptimum temperature impact on Mediterranean sclerophylls. To this end specific genetic and adaptational features of the individual species will be considered. *Quercus ilex*, for instance, appears to be less susceptible to lower temperatures than *Olea europaea*: Under the temperature conditions prevailing at Arco the estimated CO₂-uptake of *Quercus ilex* in January is 39% of that in October, which is half the reduction shown by *Olea europaea* (January: 19% of October). Impressive differences among species have been revealed by Kusumoto (1957) in his comparative study at Kagoshima, Kyushu Island, between the peritropical species *Cinnamomum camphora* (estimated CO₂-uptake in January 7% of that in October), the warm-temperate evergreen *Quercus glauca* (January: 25% of October), and the maritime-temperate *Camellia japonica* (January: 54% of October). Thorough investigations of low temperature effects on carbon uptake and utilization of Mediterranean sclerophylls like *Ceratonia siliqua*,

Myrtus communis, *Nerium oleander*, *Laurus nobilis* and *Pistacia lentiscus*, which are particularly indicative of the thermic conditons of their habitats, would help to elucidate possible limitations of dry matter production by suboptimal temperatures.

3. CONCLUSIONS

In the European part of the Mediterranean region occasional winter frost can cause injuries to sclerophyllous woody plants; prolonged periods of suboptimal temperatures lead to a reduction in carbon gain during the winter. In winter rainfall areas, where summer drought shortens the time available for efficient carbon acquisition, a second unfavourable season would further impair the annual carbon budget. However, as clearly shown by Mitrakos (1980), drought stress and cold stress - at least in Greece - are inversely correlated, so that the locations with the highest drought impact are also those with the least cold stress. A combination of the two types of environmental stress is most likely to be encountered at higher elevations of the drier regions.

In the search for criteria to quantify low temperature effects on Mediterranean sclerophylls the following may be useful:

1. For grading frost resistance and winter survival capacity of woody plants experimental *and* observational data on the susceptibility of juvenile stages and reproductive organs are necessary in addition to the usual data for leaves and shoots of adult individuals.
2. The depression of CO₂-uptake by suboptimal temperatures can be exactly determined by year-round field measurements of gas exchange rates in combination with records of microclimate, phenology, storage dynamics, and water status of the plants. There is an urgent need for long-term field measurements on selected sclerophyllous species; the only one comprehensive

research in the Mediterranean region employing modern equipment was done with *Quercus ilex* at Montpellier (Eckardt et al. 1975).

3. As a first approach, for comparatistic analyses of the specific sensitivity of metabolic responses like photosynthesis and respiration to suboptimal temperatures and cold stress, also laboratory research can be useful. Attempts are being made to develop non-expensive methods suitable for screening tests.
4. Effort should be made to recognize low temperature effects on seedling establishment, mineral uptake, growth and development of Mediterranean sclerophylls.

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1. INTRODUCTION

Solar irradiance is the fundamental energy source for photosynthesis, transpiration, and microenvironmental processes, yet measurements of solar irradiance are rare. In the mediterranean regions of the world, incoming solar irradiance has been calculated for southern California and central Chile and given by Miller et al. (1977); data for South Africa were summarized by Schulze and McGee (1978); and data for Australia were summarized by the Bureau of Meteorology (1975).

The interception and absorption of solar irradiance in the vegetation canopy is a major factor in the interactions between climate and the vegetation (Budyko, 1956; Gates, 1962, 1965). Because of its importance, many analytical models for interception have been proposed (de Wit, 1965; Anderson, 1966; Duncan et al., 1967; Miller et al., 1976; and others), and measurements have been completed in canopies of several vegetation types. Few measurements of solar irradiance in the canopies of mediterranean scrub vegetation have been published (Lawrence, 1975; Roberts and Miller, 1977), but the interception of light by the overstory shrubs has been suggested as reducing herb, grass, and shrub growth in mediterranean scrub vegetation (Bauer, 1936; Westman, 1981).

The mediterranean climate is moderate in temperature and is semiarid (Aschmann, 1973). The vegetative growing period is controlled by low temperatures in winter, which are adequate for photosynthesis but not for growth, and by soil drought in summer (Mooney and Dunn, 1970; Miller, 1979). In winter photosynthesis can be light limited (Miller and Mooney, 1976) and evapotranspiration can be radiation limited (Miller et al., 1980). In summer the onset of dry soils and high plant water stress is affected

by evapotranspiration and radiation balance. Leaf temperatures are potentially high and may be supra-optimal, especially among plants growing near the soil surface, although leaf temperatures usually do not reach lethal limits (Zohary, 1962). Soil temperatures are influenced strongly by solar irradiance.

In southern California evergreen, hard-, small-leaved shrubs predominate on rocky slopes in the elevational range of 700-1400 m and in the precipitation range of 350-650 mm/yr (Parsons and Moldenke, 1975; Miller et al., 1977). This vegetation type, chaparral, is often divided into mixed and chamise chaparral (Horton, 1941; Steward and Webber, 1980). Mixed chaparral is dominated by several species, including *Quercus dumosa*, *Adenostoma fasciculatum*, and species of *Arctostaphylos* and *Ceanothus*. The leaf area index can be up to $3.6 \text{ m}^2/\text{m}^2$ (calculated from Krause and Kummerow, 1977). Chamise chaparral is dominated by one species, *A. fasciculatum*, which is microphyllous with tightly clustered leaves and ascending stems. The leaf area index (planar area, one side) in chamise chaparral is about $1.0 \text{ m}^2/\text{m}^2$ or less (from Krause and Kummerow, 1977; Mooney et al., 1977). Within the chaparral zone mixed chaparral is more common at higher elevations on pole-facing slopes at midelevations, while chamise chaparral is more common than mixed chaparral at lower elevations and on the equator-facing slopes at midelevations.

Drought semideciduous soft-leaved shrubs and herbs predominate at lower elevations and lower annual precipitation. This vegetation type, the coastal sage, has a leaf area index of about $1.0 \text{ m}^2/\text{m}^2$ (Mooney et al., 1977). Montane forest, with conifers and broad-leaved evergreen and winter deciduous trees and an understory of shrubs or herbs, occurs at higher elevations and higher annual precipitation amounts. Matorral, composed of

evergreen, hard-leaved shrubs and short trees, occurs in central Chile at similar elevations and precipitation ranges as chaparral in California (Miller et al., 1977).

Vegetation patterns of high leaf area indices on pole-facing slopes and low leaf area indices on equator-facing slopes are common in the Northern Hemisphere. The difference is generally attributed to lower irradiance on the pole-facing slope, leading to less evapotranspiration and more favorable soil moisture conditions. However, Miller and Poole (1979) and Ng and Miller (1980) found drier soils and more prolonged soil drought on the pole- than on the equator-facing slope. Griffin (1973) and Syvertsen (1974) found lower water tensions indicating drier conditions on the pole-facing slopes in oak woodlands in northern California. Martin and Specht (1962) noted an analogous relationship in south Australia. The reversal of the common pattern may be related to the drought resistance and shade tolerance of the shrubs and the radiation and precipitation regimes in the mediterranean type climate. An analysis of canopy and soil irradiance is a first step toward explaining the soil moisture conditions on pole- and equator-facing slopes in mediterranean regions.

This paper reports measurements of incoming solar irradiance at the coast, in the chaparral, in the montane in southern California, and in the matorral in central Chile and relates these measurements to interrelations between solar irradiance and the vegetation. The interception and absorption of solar and infrared irradiance was measured in two chaparral types, mixed and chamise chaparral, and in the matorral.

2. METHODS

In California irradiance was measured at the Echo Valley Research Station in the Cuyamaca Mountains of San Diego County (116°40' W, 32°55' N; elevation 1000 m), at Camp Pendleton along the

coast 100 km north of San Diego (117°31' W, 33°21' N) and at the Mounq Laguna Observatory of San Diego State University about 100 km east of San Diego (116°26' W, 32°50' N). In Chile the measurements were carried out at Fundo Santa Laura about 60 km north of Santiago near TilTil (71°00' W, 33°04' S). The geology, topography, soil chemistry, microclimate, vegetation, and animal characteristics were described by Mooney (1977a) and Thrower and Bradbury (1977). From May 1971 to May 1974, solar irradiance was measured at all four sites with pyrheliographs. At Echo Valley and Fundo Santa Laura solar irradiance was also measured with Moll-Gorzynski solarimeters. The pyrheliographs generally recorded lower irradiance than the Moll-Gorzynski solarimeters, so the pyrheliographs were adjusted upward to standardize all records to those of the Moll-Gorzynski solarimeters. Two Moll-Gorzynski solarimeters were placed on a ridgetop. One solarimeter was shaded from the direct solar beam with a shading band (Horowitz, 1969). The Moll-Gorzynski solarimeters were calibrated periodically against an Eppley pyranometer which was maintained as a standard.

At Echo Valley and at Fundo Santa Laura, solar irradiance above and below the canopy was measured on pole-facing slopes which have azimuths of 50° (northeast) and inclinations of 19° and on ridgetops with equator-facing aspects which have azimuths of 160° (south-southeast) and inclinations of 12°. At Echo Valley the vegetative cover on the pole-facing slope and ridgetop was 102% and 63%, respectively (Ng, 1974). The pole-facing slope is covered with an almost closed canopy of mixed chaparral comprised largely of *Ceanothus greggii* Gray var. *perplexans* (Trel.) Jeps., *Quercus dumosa* Nutt., and *Arctostaphylos glauca* Lindl. The ridgetop and equator-facing slopes are covered by chamise chaparral dominated by widely spaced *Adenostoma fasciculatum* H. & A. with scattered clumps of *C. greggii*. At Fundo Santa Laura the vegetative cover on the pole-facing slope and ridgetop is about 70% and 50%, respectively. The pole-facing slope is vegetated by *Quillaja saponaria*, *Cryptocarya alba*,

Colliguaya odorifera, and *Lithraea caustica*.

The ridgetop is covered by *Satureja gilliesii*, *Trevoa trinervis*, *Colliguaya odorifera*, *Lithraea caustica*, and herbs.

Leaf and stem area indices are not easily measured in chaparral, which contain many small leaves, often closely appressed to the stem, and many small stems. At Echo Valley leaf and aboveground stem biomasses were measured in April 1978 in 2, 70-m² plots on the pole-facing slope and 1, 70-m² plot on the ridgetop. Plots were cleared of all shrubs which were weighed separately by species. Plot area was corrected to the horizontal for calculating the leaf area index. Ratios of leaf area:leaf weight were measured to convert from leaf dry weight to leaf area. In May 1979 leaf areas were reestimated by measuring the leaf area on sample branch units, estimating the number of sample branch units per shrub, and counting the number of shrubs of each species per square meter. Two people made the estimates independently. Each estimate was repeated until the two independent estimates were within 20% of each other. At Fundo Santa Laura leaf area indices were estimated in December 1979 using the same procedures and personnel used at Echo Valley in May 1979.

On each slope total solar irradiance above the canopy (S_t) and reflected solar (S_r) were measured continuously with Moll-Gorzynski solarimeters (300-3000 nm) from April 1978 to May 1979 at Echo Valley and from October 1979 to February 1980 at Fundo Santa Laura. Solar irradiance reaching the soil surface (S_{ts}) was measured with eight solarimeters. Two additional solarimeters were used to measure solar reflected from the soil surface (S_{rs}). These ten solarimeters were moved between the pole-facing slope and ridgetop periodically throughout the measurement period. Solar irradiance absorbed by the soil and canopy (S_{sc}) was calculated as $S_{sc} = S_t - S_r$, absorbed by the soil (S_s) as $S_s = S_{ts} - S_{rs}$, and absorbed by the canopy (S_c)

as $S_c = S_{sc} - S_s$.

Net radiation above the canopy was measured continuously throughout the study using Fritschen net radiometers (3000-11,000 nm). Net radiation of the soil surface was measured with four randomly placed radiometers that were moved between slopes along with the solarimeters.

Infrared irradiance from the sky was measured with a Fritschen radiometer with the bottom hemisphere covered with an insulated metal dome. The temperature of the metal dome was measured and the infrared irradiance onto one side of the radiometer thermopile was calculated using the Stephan-Boltzmann radiation law. Total downward irradiance was the sum of the net irradiance measured on the thermopiles and the infrared irradiance from the dome. Infrared irradiance from the sky was calculated by subtracting the total solar irradiance from the total downward irradiance. The solar irradiance used to calculate sky infrared irradiance was measured with a solarimeter mounted next to the net radiometer.

All solarimeters and radiometers were calibrated every 2-3 months against a 50-junction Eppley pyranometer. The changes in calibration constants never exceeded 5%. A computer controlled data acquisition system (DAS) monitored the sensor outputs. The DAS scanned each sensor 150 times in 35 min and then printed and recorded the mean values on punched tape.

3. RESULTS

At Echo Valley in 1978 the leaf and stem biomasses were 440 g/m² and 2890 g/m² in the mixed chaparral and 310 g/m² and 1310 g/m² in the chamise chaparral, respectively. The leaf biomasses converted to leaf area indices of 1.8 and 1.2 in the two chaparral types, respectively, assuming a leaf specific weight of 252 g/m² (Mooney 1977b) and adjusting for the inclinations of the slopes (Tab. 1). In May 1979, leaf area indices were estimated as 2.3 and 0.8 in the two chaparral types. At Fundo Santa Laura in December 1979, leaf area indices were

$0.66 \text{ m}^2/\text{m}^2$ on the pole-facing slope and $0.81 \text{ m}^2/\text{m}^2$ on the ridgetop. Inclusion of species not measured raises the leaf area index to about 2.1 on the pole-facing slope at Fundo Santa Laura.

TABLE 1. Leaf area indices of communities on the pole-facing slopes and ridgetop at Echo Valley and Fundo Santa Laura. a and b refer to two different plots on the pole-facing slope.

Species	Pole-facing slope		Ridgetop
<hr/>			
Echo Valley - April 1978			
<u>Quercus dumosa</u>	0 ^a	0.52 ^b	0
<u>Arctostaphylos glauca</u>	1.09 ^a	0.52 ^b	0
<u>Ceanothus greggii</u>	0.63 ^a	0.49 ^b	0
<u>Adenostoma fasciculatum</u>	0.03 ^a	0.22 ^b	1.23
TOTAL	1.75 ^a	1.75 ^b	1.23*
Echo Valley - May 1979			
<u>Quercus dumosa</u>	0.32		0
<u>Arctostaphylos glauca</u>	1.04		0
<u>Ceanothus greggii</u>	0.90		0
<u>Adenostoma fasciculatum</u>	0.00		0.81
TOTAL	2.26		0.81
Fundo Santa Laura - December 1979			
<u>Lithraea caustica</u>	0.64		0.39
<u>Colliguaya odorifera</u>	0.01		0.38
<u>Trevoa trinervis</u>	0.003		0.01
<u>Satureja gilliesii</u>	0.004		0.03
TOTAL	0.66		0.81

*uncorrected for slope

The annual receipt of solar irradiance measured on the pyrheliographs was $7,621 \pm 156 \text{ MJ m}^{-2} \text{ yr}^{-1}$ at Echo Valley and $7,621 \pm 273 \text{ MJ m}^{-2} \text{ yr}^{-1}$ at Fundo Santa Laura. Although the two sites had similar annual totals the seasonal distribution differed (Fig. 1). Irradiances averaged $3.4 \text{ MJ m}^{-2} \text{ day}^{-1}$ greater at Echo Valley than at Fundo Santa Laura during winter and $3.3 \text{ MJ m}^{-2} \text{ day}^{-1}$ less at Echo Valley than at Fundo Santa Laura during summer. Receipt of less than $4 \text{ MJ m}^{-2} \text{ day}^{-1}$ in winter was less common at Echo Valley than at Fundo Santa Laura because of less cloud cover at Echo Valley. At Camp Pendleton the annual incoming solar irradiance was 85% that at Echo Valley, while at Mount Laguna the annual solar irradiance was 89% that at Echo Valley. Solar irradiance was

depressed in May and June at Camp Pendleton because of the influx of fog and clouds from the Pacific Ocean. With respect to incoming solar irradiance Fundo Santa Laura at 1,000 m elevation is probably equivalent to elevations between 600 and 1,600 m in southern California. Solar irradiances at Camp Pendleton and Mount Laguna were not significantly different, and solar irradiances at Mount Laguna, Fundo Santa Laura, and Echo Valley were not significantly different using Duncan's test for least significant difference (Bancroft, 1968). In winter Echo Valley received the highest solar irradiance and Fundo Santa Laura the lowest; in summer Fundo Santa Laura received the highest solar irradiance and Camp Pendleton the lowest.

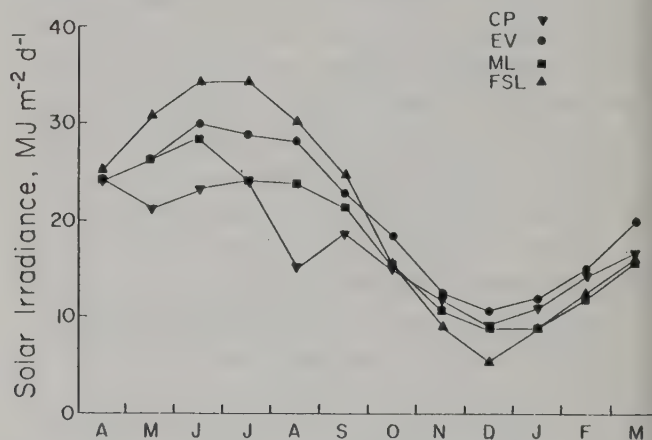


FIGURE 1. Annual progression of global solar irradiance at Camp Pendleton (CP), Echo Valley (EV), and Mount Laguna (ML) in southern California and at Fundo Santa Laura (FSL) in central Chile.

Cloud cover, indicated in these measurements by the ratio of the mean monthly solar irradiance to the maximum solar irradiance measured within the same time period, was slightly lower at Fundo Santa Laura than at Echo Valley and Mount Laguna and was highest at Camp Pendleton. At all four stations cloud cover in winter was highest, but in summer was lowest at Fundo Santa Laura. Camp Pendleton had the least variable cloud cover throughout the year.

At Echo Valley and Fundo Santa Laura the annual solar irradiance on the pole-facing slopes was 87%

and that on the ridgetops was 108% of that measured on the horizontal (Fig. 2). Relative to the horizontal the irradiance on the pole-facing slopes and ridgetops varied through the season between 71 and 95% and between 98 and 116% at Echo Valley and between 78 and 99% and between 98 and 119% at Fundo Santa Laura. The pole-facing slopes received the smaller fraction of the incoming irradiance in winter; the ridgetops received the smaller fraction in summer. Incoming irradiance on the horizontal was about 3% lower on the pole-facing slope than on the equator-facing slope because of shade from the surrounding topography in the evening. At Echo Valley the pole-facing slope received $5,380 \text{ MJ m}^{-2} \text{ yr}^{-1}$ while the ridgetop received $6,617 \text{ MJ m}^{-2} \text{ yr}^{-1}$. At Fundo Santa Laura the two surfaces received $5,736 \text{ MJ m}^{-2} \text{ yr}^{-1}$ and $6,866 \text{ MJ m}^{-2} \text{ yr}^{-1}$, respectively. The irradiance at Camp Pendleton and Mount Laguna on the horizontal was similar to the irradiance on the pole-facing slopes but was less than the irradiance on the ridgetops at both Echo Valley and Fundo Santa Laura. During summer the lower midday intensities on the pole-facing slopes were compensated by the longer diurnal period of receipt of direct solar irradiance because the sun rises and sets in the northern quadrants.

During the period of canopy measurements at Echo Valley solar irradiance varied between $31.0 \text{ MJ m}^{-2} \text{ day}^{-1}$ in June and $7.5 \text{ MJ m}^{-2} \text{ day}^{-1}$ in December (Fig. 3). Solar irradiance in September was higher than expected from the general decline of irradiance after the summer solstice, perhaps because of clear skies during Santa Ana conditions. Infrared irradiance from the sky in California varied between $25.5 \text{ MJ m}^{-2} \text{ day}^{-1}$ in winter and $29.3 \text{ MJ m}^{-2} \text{ day}^{-1}$ in late summer. Both the solar and the infrared irradiance were more variable in winter than in summer because of the intermittent storms and cloud cover. At Fundo Santa Laura solar irradiance was $29\text{--}33 \text{ MJ m}^{-2} \text{ day}^{-1}$ on clear days

and as low as $9.5 \text{ MJ m}^{-2} \text{ day}^{-1}$ on cloudy days which were common in this particular spring.

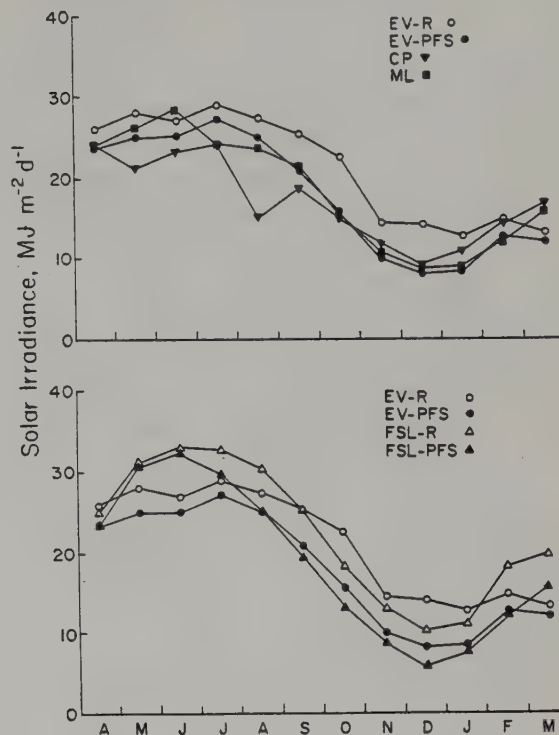


FIGURE 2. Annual progression of incident solar irradiance at Echo Valley on ridgetop (EV-R) and pole-facing slopes (EV-PFS), at Camp Pendleton (CP), at Mount Laguna (ML), and at Fundo Santa Laura on ridgetop (FSL-R) and pole-facing slopes (FSL-PFS).

Over the mixed chaparral on the pole-facing slope at Echo Valley the reflected solar irradiance was between $1.0 \text{ MJ m}^{-2} \text{ day}^{-1}$ in winter and $4.2 \text{ MJ m}^{-2} \text{ day}^{-1}$ in summer. Over the chamise chaparral on the ridgetops reflected solar irradiance was $1.0 \text{ MJ m}^{-2} \text{ day}^{-1}$ and $5.0 \text{ MJ m}^{-2} \text{ day}^{-1}$ in the comparable seasons. The solar irradiance, which passed through the canopy as unintercepted direct beam irradiance or as diffuse irradiance from the sky and intercepted irradiance scattered in the canopy, was $1.7\text{--}8.4 \text{ MJ m}^{-2} \text{ day}^{-1}$ throughout the year in the mixed chaparral and $3.1\text{--}18.0 \text{ MJ m}^{-2} \text{ day}^{-1}$ throughout the year in the chamise chaparral. The fraction penetrating the canopy was smaller and less variable in the mixed chaparral on the pole-facing slope. The soil

reflected between 0.4 and 2.5 MJ m⁻² day⁻¹ in the mixed chaparral and between 0.8 and 3.3 MJ m⁻² day⁻¹ in the chamise chaparral. The soil absorbed between 1.3 and 5.9 MJ m⁻² day⁻¹ in the mixed chaparral and between 2.1 and 13.0 MJ m⁻² day⁻¹ in the chamise chaparral. The soil fluxes are uncorrected for the inclination of the soil surface on the slopes. In both chaparral canopies the smallest amounts of absorbed solar irradiance occurred during winter. Solar irradiance absorbed in the canopy was larger in mixed chaparral throughout the year. The mixed chaparral canopy absorbed between 5.6 and 22.2 MJ m⁻² day⁻¹ while the chamise canopy absorbed between 2.1 and 13.6 MJ m⁻² day⁻¹ throughout the year.

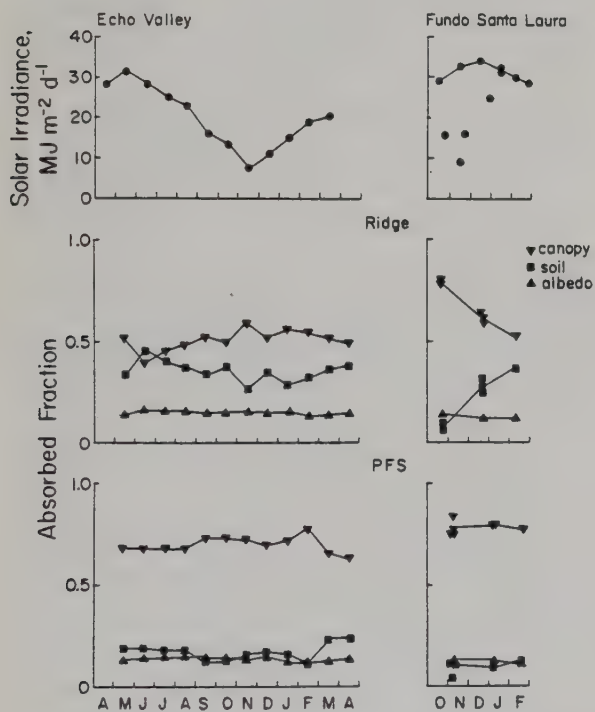


FIGURE 3. Annual progression of incoming global solar irradiance above the canopy (●) and the fractions of incoming solar irradiance reflected above the canopy (▲), absorbed in the canopy (▼), and absorbed in the soil (■) on the pole-facing slopes (PFS) and ridgetops.

In terms of the fractional partitioning of

incoming solar irradiance, the albedo was 11-12% over mixed chaparral and 12-13% over chamise chaparral. Albedos were higher in summer. The fraction absorbed in the canopy varied from 62 to 76% in mixed chaparral and from 40 to 58% in chamise chaparral. The fractions absorbed were highest in winter. The fractions absorbed by the soil varied opposite to the fractions absorbed by the canopy and were lowest in winter. The fraction absorbed by the soil varied from 11 to 22% in mixed chaparral and from 26 to 45% in chamise chaparral.

The partitioning of solar irradiance was similar in the matorral at Fundo Santa Laura. The albedo was 12-13% over matorral on the pole-facing slope and ridgetop. The fraction absorbed in the ground was 4-13% on the pole-facing slope and 7-9% on the ridgetop.

Net total irradiance followed the annual course of incoming solar irradiance (Fig. 4). Over bare ground, net irradiance on the pole-facing slope was about 70% of that on the ridgetop with a greater difference in winter than in summer (Miller et al., 1977). Net irradiance above the canopy was 1.0-3.1 MJ m⁻² day⁻¹ in summer and 1.7 MJ m⁻² day⁻¹ in December. Net irradiance absorbed in the canopy was higher in mixed chaparral. About 75% of the net irradiance above the canopy was absorbed in the mixed chaparral canopy and about 50% was absorbed in the chamise chaparral canopy. The net irradiance absorbed in the canopy was 1.7-15.9 MJ m⁻² day⁻¹ in mixed chaparral and 0.6-11.5 MJ m⁻² day⁻¹ in chamise chaparral. The net irradiance absorbed in the soil was 0.2-4.2 MJ m⁻² day⁻¹ in mixed chaparral and 1.0-13.0 MJ m⁻² day⁻¹ in chamise chaparral.

The net loss of infrared irradiance was similar in mixed and chamise chaparral and was 4.2-9.4 MJ m⁻² day⁻¹. In both most of the infrared loss was from the canopy, especially in winter. The net infrared at the soil surface was 0 to -2.1 MJ m⁻² day⁻¹ in mixed chaparral and was +1.3 to -5.0 MJ m⁻² day⁻¹ in chamise chaparral. Net infrared at the soil surface was expected to be closer to zero in mixed chaparral because of the more closed canopy.

In mixed chaparral infrared irradiance loss accounted for 57% of the incoming solar, 59% of the solar absorbed in the canopy, and 67% of the solar absorbed in the soil. In chamise chaparral infrared irradiance loss accounted for 63% of the incoming solar irradiance above the canopy, 75% of the solar absorbed in the canopy, and 39% of the solar absorbed in the soil.

2 for different mediterranean type regions.

In southern California the geographic pattern of incoming annual solar irradiance at the coast and mountains and on the slopes at the chaparral site corresponds with the geographic and topographic distribution of several widespread species or genera, including *Quercus dumosa* and *Leaenothus* which occur on a diversity of slope exposures at the coast and

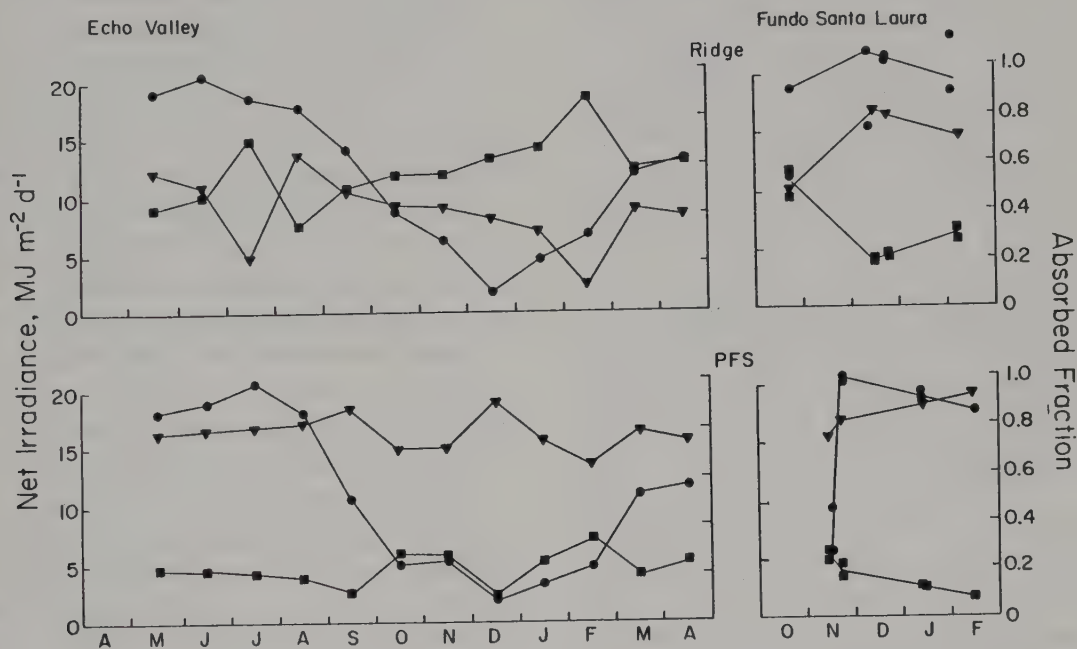


FIGURE 4. Annual progression of the net total irradiance measured above the canopy (●), and the fraction absorbed in the canopy (▼), and soil (■) on the pole-facing slopes and ridgetops.

4. DISCUSSION

The leaf area indices at Echo Valley and Fundo Santa Laura are similar to those in other mediterranean regions. Jones (1968) measured seasonal variation in leaf area indices between 1.8 and 3.2 in Australian heathland. Lossaint (1973) gives a leaf area index of 4-5 for the *Quercus ilex* forest and about 1.6 for *Quercus coccifera* garrique in south France. Miller et al. (unpublished) estimated leaf area indices of 1-2 in most communities in mediterranean regions with precipitation of 400-700 mm/yr. Cody and Mooney (1978) gave values between 1 and

higher elevations but usually on north-facing slopes at midelevations (Steward and Webber, 1980).

The partitioning of incoming solar irradiance into that absorbed and that lost by infrared irradiance by the canopy and soil is predictable throughout the year. The absorption of solar irradiation is a nearly constant fraction throughout the year, a characteristic which has been related in mediterranean climates to plant water relations and photosynthesis (Orshan, 1963; Jones, 1968; Mooney and Dunn, 1970). The variation in absorbed solar irradiance in mixed and chamise chaparral and

in the pole-facing matorral is largely because of the changing path length of the solar beam through the canopy as the solar altitudes change through the year. The greater absorption of solar irradiance in the canopy in winter, compared with summer, decreases the absorption in the soil during winter. The normally low incoming solar irradiance is decreased further at the soil surface by the increased canopy absorption, which accentuates low soil temperatures under mixed chaparral. On the ridgetop at Fundo Santa Laura leaf drop by *Colliguaya odorifera* decreased the absorption of solar irradiance in the canopy. The inclination of the surface further attenuates the intensity of the absorbed irradiance.

The absorption of solar irradiance in the canopy is described by mathematical models (de Wit, 1965; Anderson, 1966; Duncan et al., 1976). These models describe the interception of solar irradiance in terms of the negative exponential equation

$$I_z = I_o [1 - \exp(-K A)]$$

where I is the irradiance at level z or above the canopy (subscript o), K is the extinction coefficient, and A is the leaf area index. An extinction coefficient of 0.7, which was used by van Keulen (1975) for calculating the absorption of solar irradiance on a daily basis, gives interrupted irradiances in the canopies of 75% of incident with a leaf area index of 2 and of 50% of incident with a leaf area index of 1, which are close to the measured absorbed irradiances of the mixed and chamise chaparral canopies, respectively, and are within the error caused by uncertainties in measuring the leaf area index. Models to calculate irradiance during the day include several additional variables. The extinction coefficient varies with solar altitude, thus, throughout the day and year, and with the angles of inclination of the leaves and stems. The success of the simplistic equation in chaparral indicates that

the details of leaf area, stem area, leaf and stem inclination, and leaf and stem clustering largely cancel each other when considering irradiances on a daily basis. The effect of the clustering of leaves and stems is compensated by the stem area. The stem area is largely shaded by leaf area. The success also indicates that the inclination of the slope affects the intensity of absorption of solar irradiance at the soil surface only; the absorption in the canopy is independent of slope.

The difference in vegetative cover and species composition on pole-facing slopes and on equator-facing slopes and ridgetops must be due to differences at the soil surface or in the soil and to the germination and establishment of individuals on bare soil rather than to differences in the absorption of irradiance in the canopy of mature vegetation. Such conditions occur after fire. Although the absorbed solar irradiance on bare soil is lower on pole- than on equator-facing slopes because of the inclination of the surface to the sun, the absorbed solar irradiance by the mature canopy can be greater because of larger leaf area indices. At Echo Valley the leaf area index of mature canopies is probably controlled by the shade tolerance of the species and by different water availability results from differences of soil evaporation which vary with soil surface temperature and solar irradiance. The bare soil surface of the pole-facing slope will be cooler and more moist and will radiate less infrared than the soil of the equator-facing slope. Conditions for establishment of seedlings should be more favorable on the north-facing slope even though the soil moisture conditions under the mature mixed and chamise chaparral stands are similar (Miller and Poole, 1979; Ng and Miller, 1980; Miller and Poole, unpublished).

The canopy develops a leaf area index consistent with the species shade tolerance and water requirements. Simulations of canopy production with increasing leaf area index indicated that maximum production with increasing leaf area index

indicated that maximum production should occur with leaf area indices of 2.5-3.5 for *Ceanothus greggii* and *Arctostaphylos glauca* and 1.0 for *Adenostoma fasciculatum* at Echo Valley and with leaf area indices of 1-2 for the four species studied at Fundo Santa Laura (Miller and Stoner, 1979). These leaf area indices are similar to the leaf area indices which now occur at these sites. The greater leaf area on the pole-facing slope at Echo Valley increases transpiration rates when water is available, dries the soil earlier, and increases the length of the summer drought so that the length of the summer drought is similar on both pole- and equator-facing slopes (Miller and Poole, 1979; Ng and Miller, 1980). Apparently, the drought duration tolerance of all evergreen shrubs is similar as might be expected since the species coexist. The leaf area index is also constrained by the transpiration rate and photosynthetic rate per unit of leaf area. The leaf area of chaparral can increase until the transpiration rate per unit of leaf area is about 150-200 mm/yr (Poole and Miller, in press). This amount of transpired water supports a carbon uptake to maintain and replace the necessary leaf, stem, and root biomass.

5.0 CONCLUSIONS

1. Incident solar irradiance at the coast, in the montane, and on the pole-facing slopes are similar. Incident solar irradiance on the equator-facing slopes is greater.
2. Interception of solar irradiance in mature mixed and chamise chaparral on pole-facing slopes and ridgetops is similar.
3. After establishment leaf area index increases toward an optimal leaf area for production, toward a value which reduces water use per unit leaf area to about 150-200 mm/yr, or toward a leaf area which increases length of drought to 100 days. These three constraints seem to apply in southern California.

4. Distribution of species seems correlated with conditions and requirements during the establishment phase, not with conditions during the mature phase of vegetation development.

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TEMPERATURE GERMINATION RESPONSES IN THREE MEDITERRANEAN EVERGREEN SCLEROPHYLLS*

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Distribution data of the mediterranean evergreen sclerophylls along summer drought and winter cold stress gradients in Greece (Mitrakos 1980), do not support current views (Dunn et al. 1976) concerning their convergent evolution under Mediterranean climatic conditions.

On the other hand, seed ecophysiological work (Thompson 1971, Argyris 1977) suggests that optimal temperatures for seed germination of mediterranean species are around 15°C and that at temperatures higher than 20°C germination is slow or ceases at all. Thus, under natural conditions, seeds of mediterranean species germinate during autumn, when temperatures are optimal and water is available.

Seeds were collected during 1979 from plants around Athens. The two former species were wild growing while the latter planted. Seeds were stored under ambient conditions. Germination tests were conducted in petri dishes or plastic containers, lined with filter paper under saturated conditions of humidity. Seeds of *C.siliqua* were previously treated with 95-97% sulphuric acid for one hour. Experiments were performed at 15.0, 20.0, 25.0, 27.5, 30.0 and 35°C and germination was recorded daily until the 15th day after sowing, except for a few cases where it was followed up to the 20th day. Temperature variations, recorded by a thermograph, were smaller than $\pm 1^\circ\text{C}$. The mean's standard errors are given graphically.

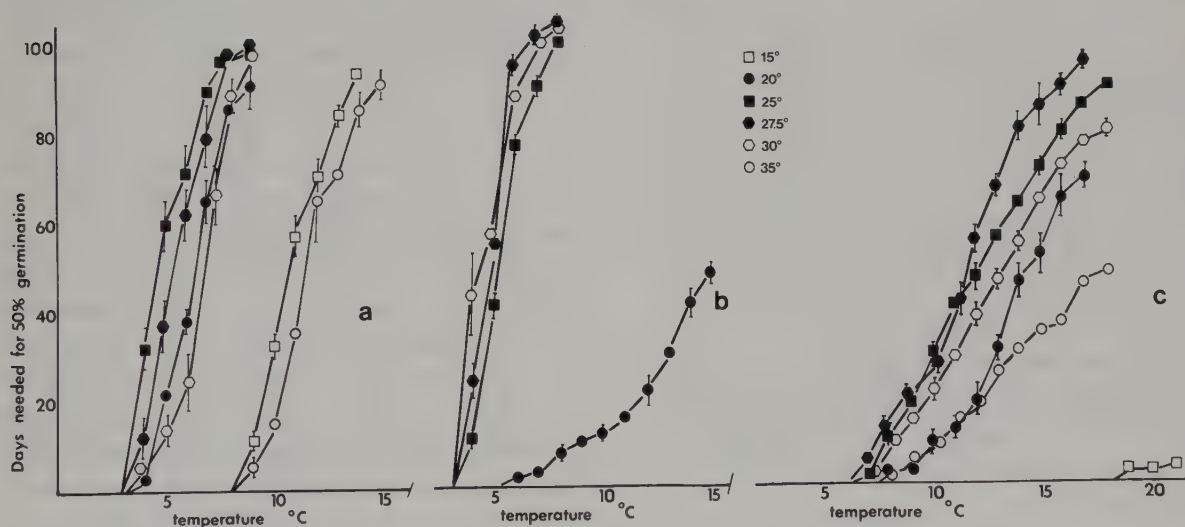


FIGURE 1. Germination curves for *C.siliqua* (a), *N.oleander* (b) and *M.communis* (c), at different temperatures.

In this paper we present data concerning the temperature dependence of seed germination in three evergreen sclerophylls, i.e. *Nerium oleander* L., *Myrtus communis* L. and *Ceratonia siliqua* L.

Obtained germination curves (Fig.1) show clearly that optimum temperatures are around 27.5°C, at which final germination levels are 95-100% within 6, 7 and 17 days for *C.siliqua*, *N.oleander* and *M.communis* respectively. The rates of germination are generally high at temperatures from 20 to 30°C. Seeds of *N.oleander* germinate slowly at 20°C and

*This paper is dedicated to 75th birthday of Prof.E.Bunning, Tübingen, W.Germany.

fail to germinate at both 15°C and 35°C. Seeds of *M. communis* and *C. siliqua* germinate slowly at 15°C and with relatively higher rates at 35°C. In order to understand to what extent this temperature germination responses correlate with the mediterranean climate, we first calculated, from the germination curves (Fig.1), the number of days needed for 50% germination for each one of the three species under each different temperature (Table 1).

TABLE 1. Days needed for 50% germination at different temperatures.

Temp. °C	15.0	20.0	25.0	27.5	30.0	35.0
Species						
<i>N. oleander</i>	-	15.0	5.0	4.5	5.0	-
<i>C. siliqua</i>	11.0	6.5	6.0	5.5	6.7	11.5
<i>M. communis</i>	-	14.8	12.1	11.7	13.5	18.0

To have an estimate of the temperature germination responses under field conditions, we replace the constant temperatures of our experiments with the mean monthly air temperatures of Argostolion, a town on the island of Cephallenia, where the three species grow wild (Fig.2). In this way, we obtained a kind of "character curves" (Tompson 1973) which indicate the days needed for 50% germination at the different months, under natural conditions. These curves are drawn on the stress diagram of this station (Mitrakos 1980), in order to correlate the temperature germination responses with the drought and cold stress of the area.

Fig.2 shows clearly that optimal germination temperatures exist from June to September, during this period no water is available for germination. The temperatures prevailing from September to November would promote germination while during this period water is also available. Therefore it could be suggested that the seeds of the three species do germinate during these months and the seedlings survive during the winter. In May

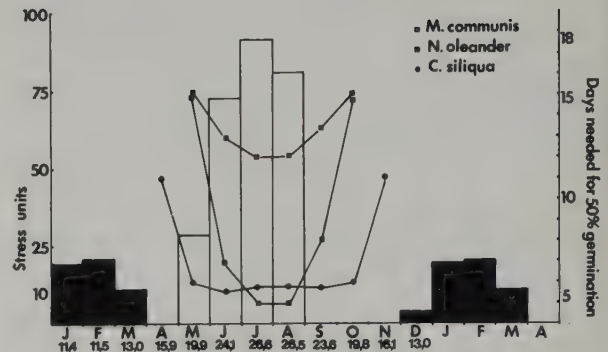


FIGURE 2. Temperature germination responses of *C. siliqua*, *N. oleander* and *M. communis* at different months. Right handside ordinate represents days needed for 50% germination. Left handside ordinate represents arbitrary stress units for cold (black columns) or drought (white columns). Numbers below each month (on the abscissas) represent mean monthly temperature.

and April seeds of the three species, especially those of *C. siliqua*, could germinate, but seedling survival during the following drought period is problematic. In areas drier than Argostolion, the summer drought is extended in September or even to the middle of October and the winter is usually warmer. The period favourable for seed germination is shifted towards the winter, as may be seen from the following typical meteorological records which refer to Hierapetra, a town on the island of Crete (Table 2). A period favourable for germination exists also during the first two spring months, but seedling survival during summer is again likely to be problematic. Areas with a shorter summer drought, offer almost ideal conditions for seed germination during summer, as in the case of Ioannina, a town in the north-western mainland of Greece (Table 2). Interestingly, the three species are not found in this area, and we can assume that the winter of Ioannina is too severe, at least for seedling survival.

TABLE 2. Monthly mean air temperature ($^{\circ}\text{C}$) and precipitation (mm) for Hierapetra and Ioannina.

Month	Hierapetra		Ioannina	
	$^{\circ}\text{C}$	mm	$^{\circ}\text{C}$	mm
Jan.	13.0	147.3	5.2	162.6
Feb.	13.3	72.1	6.3	134.0
March	14.7	49.1	9.0	104.0
April	17.3	21.6	13.9	85.0
May	21.0	11.3	17.5	77.3
June	25.8	1.2	22.2	57.4
July	28.3	0.0	25.5	31.8
Aug.	28.1	0.5	25.0	26.2
Sept.	25.1	5.9	20.6	56.6
Oct.	21.7	48.1	15.3	129.3
Nov.	18.3	70.4	10.4	174.3
Dec.	14.8	120.9	6.7	197.7

Data presented make it clear that the three species retain the germination behaviour they had before the mediterranean climate was established, i.e. when summer was wet and the winter milder (Axelrod 1973, Mitrakos 1980). It means furthermore that these species are not mediterranean, at least as far as it concerns their seed adaptive strategies. Indications exist that *Olea* seeds also show similar, although more complicated, response to temperature (Diamantoglou and Mitrakos 1979).

Argyris (1977), reported detailed data concerning seed germination and seedling survival in *Phlomis fruticosa*, *Euphorbia acanthothamos*, *Thymus capitatus*, *Cistus creticus* and *Sarcopoterium spinosum*. For all these phrygantic species, optimum temperature for seed germination is around 15°C . Data obtained so far on temperature germination responses in phrygantic species and evergreen sclerophylls indicate a qualitatively different behaviour of the two groups (Fig.3).

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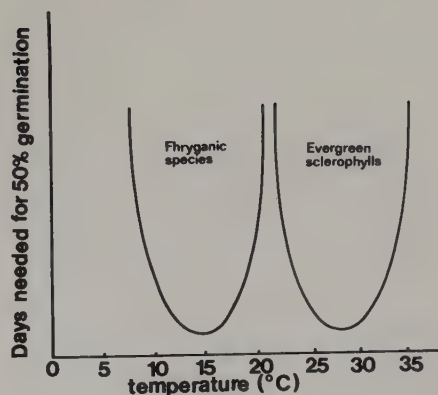


FIGURE 3. Generalized scheme for temperature germination responses of Phrygana and Evergreen sclerophylls.

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